TEMPORAL VARIATION IN SPACE AND RESOURCE USE OF MACAWS IN THE SOUTHEASTERN PERUVIAN AMAZON

A Thesis

by

KRISTA ANNE ADAMEK

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

May 2011

Major Subject: Wildlife & Fisheries Sciences

Temporal Variation in Space and Resource

Use of Macaws in the Southeastern Peruvian Amazon

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Approved by:

Chair of Committee,	Thomas E. Lacher, Jr.
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ABSTRACT

Temporal Variation in Space and Resource Use of Macaws in the Southeastern Peruvian Amazon. (May 2011)

Krista Anne Adamek, B.S., University of British Columbia

Chair of Advisory Committee: Dr. Thomas Lacher, Jr.

Space use and resource use of three species of macaws (*Ara ararauna*, *A. chloropterus*, and *A. macao*) were studied for a period of three years in the southeastern Peruvian Amazon. Basic information on wild macaw populations is lacking due to the logistical and behavioral challenges of working with these species in dense rainforest. Population declines world-wide have been attributed significantly to a reduction in food and nesting resources due to habitat loss. This research aims to obtain baseline data on macaws in a region with relatively intact rainforest. Specific objectives were to (1) quantify space use, describe the spatial and temporal variation in movement patterns, explore habitat selection and spatial pattern of resources during the non-breeding season, and (2) identify key nesting and foraging species and determine whether there is seasonal variation in diet, and explore how resources may be related to movements and competition.

Individuals from each species were radio-tagged and monitored from 2004 to 2008 by ground, platform, and aerial tracking. Seasonal ranges were estimated using MCP and KDE methods. Diversity and niche measurements and selection were

calculated for dietary items, nesting substrate, and habitat. The relationship between palm habitat distribution and *A. ararauna* movements was explored using landscape analysis techniques.

All species had similar home range sizes during the breeding season, ranging from a mean of 1,540 ha to 2,541 ha. Non-breeding ranges were significantly larger for *A. ararauna* (117,849 ha). Greater than 200 species of plants were consumed, yet seasonal preferences vary. The increase in dietary breadth and decrease in overlap during dry season is unlikely related to food scarcity or competition. Key nesting and dietary species include *Mauritia flexuosa*, *Dipterix micrantha*, and *Bertholletia excelsa*. Palm habitat is a key resource for *Ara ararauna* and associated with long-distance movements.

This research addresses a critical gap in our knowledge regarding macaw movements and resource use in Amazonian rainforest. Despite their mobility, their low fecundity and specialized nesting requirements can impact reproductive success and population growth if habitat loss continues on its current trajectory.

DEDICATION

This is dedicated to Nena,

and Jota5,

and all of their feathered friends

of all colors, large and small

in the Madre de Dios.

ACKNOWLEDGEMENTS

I would like to thank my committee chair, Dr. Tom Lacher Jr., for his patience, wisdom and well-timed advice. His knowledge knows no bounds. What I've learned is more than just tropical biology and conservation; he is a great role model as well. I would also like to thank my committee members for their support and helpful insights. Dr. Lee Fitzgerald inspired me always think about the "science" part in conservation science and challenged me with good questions. I appreciated Dr. Feagin's love for ecology and his creativity in exploring relationships of wildlife and landscapes. As a whole, I am thankful to everyone for keeping me on track as I continuously generated questions that were beyond the scope of this work. Finally, I'd like to thank Dr. George Powell for his encouragement to pursue this degree, his dedication for macaws and their conservation, and his enduring passion to know more and do more.

Within the department of Wildlife & Fisheries, so many people were instrumental to my success in this endeavor. I'd like to extend my gratitude to all the office gals for their generosity, and especially to Shirley who kept tabs on all of us. Thank you to Felix for his guidance and rescues through the paperwork maze. Tariq was always happy to assist me with many of my computer issues. I particularly liked the open doors where one could pop in to chat. Dr. Grant gave me the opportunity to philosophize over things beyond my research, and a chance to practice my Spanish. I would also like to thank all the TA coordinators for allowing me a very rewarding and new experience of teaching.

It was a pleasure to interact with so many people from different departments and backgrounds. In particular, Dr. Ben Wu and Dr. Popescu provided my first official introduction to landscape interpretation. Dr. Brightsmith was a harbinger of macaw stories. I was also fortunate to be part of the Applied Biodiversity Sciences family of professors and students with interests and experience both similar and different to mine.

Of course, none of this would have been possible without the generous financial and logistical support of so many entities. I am grateful to the World Wildlife Fund for providing financial support for this long-term project, and to the Gordon and Betty Moore Foundation for their generous donation in support of tropical conservation. I would also like to thank INRENA (Instituto Nacional de Recursos Naturales) for providing us permits, and the local communities for welcoming the odd people with big antennas. ACCA (Asociación para la Conservación de la Cuenca Amazónica) provided working and living space for research activities, and in particular I'm grateful to Jesus Ramos for his unfailing logistical support and friendship. Rainforest Expeditions also supported our research interests and provided facilities for some of our activities. I extend a sincere gratitude to the flight services provided by SAMAIR (South American Mission AIR) and Aérocondor, the mechanics that maintained the planes, and especially to the pilots for braving the remote conditions, unpredictable weather, and their incredible skill in handling the plane while tracking. In particular, I'm grateful to Craig and Carlos for our safe returns, and also to my brother, Thomas Adamek, who perhaps had the toughest job of all: piloting an Ultralight with his sister telling him what to do. His assistance with all things technical, mechanical, electrical, and solar, was invaluable.

For the copious amounts of data collected, I am eternally indebted to all the assistants who heroically and happily withstood the long hours, bugs, wetness, coldness, heat, and extended time away from their families. In particular, I'd like to acknowledge my team for their many years of dedication to the project, and their genuine love for macaws: Mario Albites, Juan Alberto Escudero, Segundo Immundo, Julio Quispe, Ivan Sandoval, and Silver Sandoval. I'm grateful to the duo of Cintya and Arnaldo, and Karim who were experts at juggling the complexities of changing project needs with practical realities. George and Sue were exemplary people that devoted their lives to conservation, living conscientiously yet selflessly, and proved challenging to keep up with. Mathias and Esperanza fall into this category as well. I will always be grateful to Raul and Paola for unleashing a beautiful love story in the midst of a difficult time. For their passion for *aguajales*, and the Madre de Dios, I hope that the BRIT (Botanical Research Institute of Texas) team will always be able to continue their research. Finally, I've come across no person wiser in life and the natural world than my Costa Rican colleague, Ulises Alemán.

On this side of the world, I thank Fred at Holohil, who developed the first macaw transmitters, and was always quick to respond to last-minute requests. The very large classified satellite image provided by Tim Killeen was an essential component of my habitat map. Steve Cane took pity on my little laptop and provided me a trustworthy computer during the final stage of my writing. A travel grant from the Ecology and Evolutionary Biology (EEB) made it possible to share the results at the Parrots International Conference.

Many people made my experience at Texas A&M rewarding by providing advice and balance. Magui was a beacon of strength and perspective who also taught me how to prepare maté the proper way. The trio of Zach, Miguel, and Alexa were my pseudo-lab mates early on and kept me healthily distracted with extracurricular activities. With Jason and Paige, we managed a few early morning mountain bike rides. Outside this circle of existence, Mike and Mike, Nicole, Chris, Nick and everyone else from other corners of campus were there to expand my horizons. The Holik Dinner Club (Chouly, Carmen, Katie, Fionna, Liz) became a wonderful tradition of sharing stories and food.

And closer to home, thank you to my mother and father for their encouragement, support and love in general, and especially in the longest hours of the final stretch. To my grandparents, I still hope to make them proud even though I didn't follow in their footsteps. I will wear a dress one day. My brother, who is also playing with robots for his own Master's degree, managed to convince me to take his old car off his hands. My primary mode of transportation however was by bicycle. Luna was a new addition last summer where I met cyclists from all over North America with unique perspectives and energizing spirits: particularly, Lars, Joey and Fionn, Adventure Cycling, and Byron the mad potter. Eileen Fielding and Robert provided a wonderful environment to write and assimilate the five years of field research. I admire their bravery to jump into something with only a dream to go by. Finally, my last gesture of appreciation goes to my little vegetable garden which amazingly thrived in the crisp mountain air and provided hours of therapeutic breaks and a place to throw my dirty dishwater.

NOMENCLATURE

AA	*Ara ararauna*
AC	*Ara chloropterus*
AM	*Ara macao*
BR	Breeding
D	Dry season
DW	Transition from dry to wet season: October
HREF	Reference bandwidth (ha) for KDE
KDE	Kernel Density Estimator
LA	Los Amigos
LSCV	Least Squares Cross Validation
MCP	Minimum Convex Polygon
N	Nesting season: November-April
NB	Non-breeding
NN	Non-nesting season: May-August
PN	Pre-nesting season: September, October
W	Wet season
WD	Transition of wet to dry season: April

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CHAPTER I

INTRODUCTION TO SPACE USE

Determining "where animals are, why they are there, and where else they could be" (Aarts et al. 2008) are critical questions for the conservation of wildlife populations. For wide-ranging species such as macaws, understanding the variation in spatial and temporal scales at which an animal moves across the landscape (Kie et al. 2002; Boyce et al. 2003; Johnson et al. 2004) is particularly important when habitat loss threatens connectivity of the landscape (Saunders et al. 1991) and can provide valuable insight for predicting responses of the animals to landscape alterations in the future (Olden et al. 2004).

Space use is closely tied to resource use (Buskirk and Millspaugh 2006; Clark and Strevens 2008) and since animal movement is rarely random, there is an underlying link between the spatial arrangement of resources on the landscape and the response of animals to these resources (McIntyre and Wiens 2000; Chesson 2000). There is increasing evidence that it is not just fine-scale presence of resources, but rather the spatial configuration of these patches across the landscape that influence animal movements (McIntyre and Wiens 2000), especially for animals with wide-ranging movements that vary seasonally (Boyce 2006; Johnson et al. 2006).

This thesis follows the style of Biological Conservation.

According to Birdlife International (Snyder et al. 2000), parrots have the highest proportion of extant threatened species (28%) of any major avian family. The principal threats include introduced predators and competitors, loss of habitat, hunting, and capture for trade (Vaughan 1983; Forshaw 1989; Vaughan et al. 1991; Beissinger and Bucher 1992; Collar and Juniper 1992; Ortiz 1995; Inigo-Elias 1996, 2000; Hesse 2000; Wright et al. 2001; González 2003; Faria et al. 2008). Among the large macaws, 7 of eleven extant species are considered threatened, and of those, 2 species have not been documented in the wild for several decades. To date, 5 species have gone extinct (Snyder et al. 2000).

Although macaws are highly mobile, recent studies report that larger forest birds may not thrive in a landscape of small patches of habitat (Uezu et al. 2005) and that a large block of suitable habitat may be critical for long-term survival (Nunes and Galetti 2007). Within one of the richest regions of the tropical Andes (Killeen et al. 2007), expansion of large-scale infrastructure is already beginning to change the landscape (Shoobridge 2006). Roads, which facilitate activities such as logging, hunting, mining, and colonization, as well as wildfires and disease, pose significant threats to biodiversity and ecosystems (Laurance 1998; Forman and Alexander 1998; Laurance 2007).

Since macaws are slow to mature, exist at low densities and have low fecundity (Forshaw 1989; Thiollay 1989; Gilardi and Munn 1998), they would be slow to recover from population declines (Renton 2004; Faria et al. 2008) and their large body size, slow generation time and habitat specialization are associated with higher extinction risk (Bennett and Owens 1997; Owens and Bennett 2000). Research on macaw populations

has been focused on activity patterns (Gilardi and Munn 1998), natural history, habitat use (Gilardi 1996), feeding ecology (Ragusa-Netto and Fecchio 2006; Vaughan et al. 2006a; Renton 2006; Berg et al. 2007; Contreras-González et al. 2009), nesting ecology (Renton 2004; Brightsmith 2005), clay lick use (Burger and Gochfeld 2003; Brightsmith and Munoz-Najar 2004), reproduction or reintroduction (Nycander et al. 1995; Oehler et al. 2001; Vaughan et al. 2003; Brightsmith et al. 2005), population estimates (Casagrande and Beissinger 1997; Renton 2002; Karubian et al. 2005), and harvesting (Beissinger and Bucher 1992; González 2003).

It has been observed that macaws require large areas and fly long distances (Casagrande and Beissinger 1997), but due to inaccessibility and behavioral characteristics of macaws themselves (Casagrande and Beissinger 1997; Gilardi and Munn 1998; Renton 2002), there exist no quantitative data on movements or space use of wild macaws in the Amazon.

Previous studies report local temporal fluctuations of parrot populations (Saunders 1980; Smith and Moore 1992; Renton 2001, 2002; Karubian et al. 2005); however, these studies lack the spatial context which is critical to the understanding of how an animal interacts with the landscape (Levin 1992). Capturing the full spatial range of landscape use will provide important information on space use of macaws which has not yet been documented, without which activities such as reserve planning can be compromised (Karubian et al. 2005).

The purpose of this study is to obtain data on wild macaws that inhabit a changing landscape to provide baseline spatial information while their habitat is still

relatively intact. It will be difficult to design effective conservation plans for macaws without knowledge of space use, and is a necessary first step that enables answering other questions about temporal and spatial variation of resource use.

METHODS

Study area

The study area encompasses a circular area of 160 km radius from the confluence of the Madre de Dios River and Los Amigos River in the department of Madre de Dios (Fig. 1). This extent was determined by the furthest recorded movements of marked macaws from the principal site where nesting and research activities occurred (Centro de Investigación y Capacitación Rio Los Amigos) (UTM: 380500E 8610297N). The majority (82%) of Madre de Dios is lowland tropical forest less than 500 meters above sea level (masl) and the Los Amigos Conservation Concession ranges from 222-437 masl (Pitman 2008). Dissecting this landscape are meandering and braided rivers of varying sediment loads, streams, oxbow lakes and swamps. Major rivers in the area are the Madre de Dios, Colorado, Iñambari, Tambopata, Piedras, and Manú.

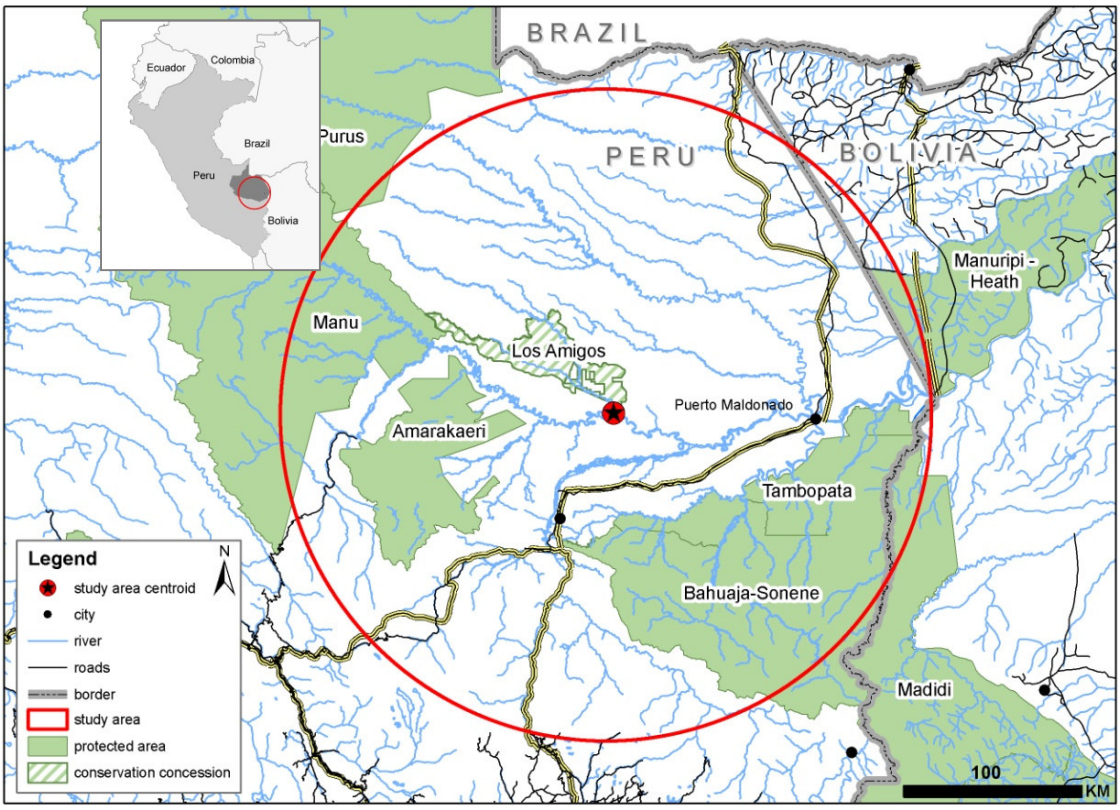

Fig. 1. The study area in southeastern Peru is within the department of Madre de Dios (inset) and part of the Amazon basin. Research activities were based out of CICRA (Centro de Investigación y Capacitación Rio Los Amigos) and extended throughout the study area (red circle) according to the movements of tagged macaws.

The Madre de Dios watershed is one of the wettest regions of the Amazon basin where annual precipitation can exceed 4,000 mm (McClain and Naiman 2008). In general, precipitation increases from east to west (Hamilton et al. 2007), and seasonality becomes more marked from north to south (Gentry and Ortiz 1993). Mean annual rainfall recorded by the weather station at CICRA between 2000-2006 was between 2,700 and 3,000 mm, with a maximum of 3,498 mm in 2003, and a minimum of 2,152 mm in 2005 (Pitman 2008). The wet season (October-May) receives over 80% of the

annual rainfall, where January is the rainiest month (Pitman 2008), and dry season extends from May-September, with August being the driest month.

The dry season is also characterized by events called “friajes”, first reported in 1992 (Morize 1922) and again in 1942 (Serra and Ratisbona 1942) which are caused by the movement of polar air masses from the south, resulting in change of climatic conditions in Amazonia and southeastern Brazil (Marengo et al. 1997). These events, which can produce frost in some areas, last between 3-5 days, and occur frequently (Culf et al. 1996). Cold fronts (“friajes”) occurred from May through September with temperatures generally below 15°C and as low as 10°C. The number of events from 2004-2008 ranged from 5-10 per dry season and lasted from 3-7 days. Between 2005 and 2007, Pitman (2008) described 14-17 “friajes” (daily minima < 20°C) and 4-5 severe “friajes” (<15°C) per winter.

This region is dominated by broadleaf evergreen or semi-evergreen tropical forest (Osher and Buol 1998). The landscape of southwestern Amazon is generally classified into two broad categories: upland forest (terra firme) and lowland forest (flooded, seasonally flooded). Two kinds of uplands were categorized based on physiography: terraced uplands which are flat and lightly dissected by small streams, and hilly uplands which are highly dissected and extend north and northwest for hundreds of kilometers (Foster 2001). Within these categories, other vegetation consists of bamboo thickets (Hamilton et al. 2007), palm swamps (Kalliola et al. 1991), tropical savannah, and extensive floodplains of varying successional stages (Kvist and Nebel 2001). This

region is also characterized by clay licks (Emmonds and Stark 1979) which are commonly associated with river-edges, although they can also occur in forested regions.

Considering the Amazon has greater than 30,000 species of plants (Gentry 1982), and is a mosaic of varying precipitation patterns, soil types, topography, hydrology, and geological history, great effort is being devoted to distinguishing vegetation types. Satellite imagery and remote sensing has revealed that there may be hundreds of unique forest cover types in the Peruvian Amazon alone (Tuomisto et al. 1995).

This is a relatively undisturbed and sparsely populated region, yet colonization of mid and lower elevations is increasing (Mena et al. 2006), spurring concern for this highly biodiverse area (Tuomisto et al. 1995; Tuomisto 1998; Patterson et al. 1998; Macquarrie 2001; Goulding et al. 2003). Currently, land use in the area is a mixture of small private land-holdings, small-scale agricultural fields, pastures, small communities, mining concessions and forest concessions; most of which are concentrated along major waterways and the Interoceanic highway, of which this last frontier section is currently being paved. A network of protected areas and indigenous reserves is bisected by the Interoceanic highway which connects Brazil with the Peruvian coast.

Data collection

To capture the full spatial and temporal range of space use by macaws, we radio-tagged and monitored the movements of three species for a period of 3 years. At Los Amigos, a total of 17, 25 and 8 individuals of *A. ararauna*, *A. chloropterus*, and *A. macao* were tagged. All *A. ararauna* and *A. macao* were captured from nests. Two

individuals of *A. ararauna* were juvenile – all other individuals of all species were adult birds. Of the 25 individuals of *A. chloropterus*, 8 were nesting individuals and 15 were of unknown breeding status tagged in the proximity of the clay lick. During the non-breeding season, an additional 3 *Ara chloropterus* apparently competing over cavities in two *Dipterix* trees along the Madre de Dios River were also tagged. An additional 17 individuals of *A. ararauna* were tagged at three other locations within the study area (Fig. 2) to determine if their seasonal movements were similar to those of the macaws monitored at Los Amigos. Nest searches were conducted between October and January, and all breeding season captures occurred between January and April. Captures at nesting cavities were accomplished using customized nest traps, and in the vicinity of the clay lick using mist nets installed in the canopy.

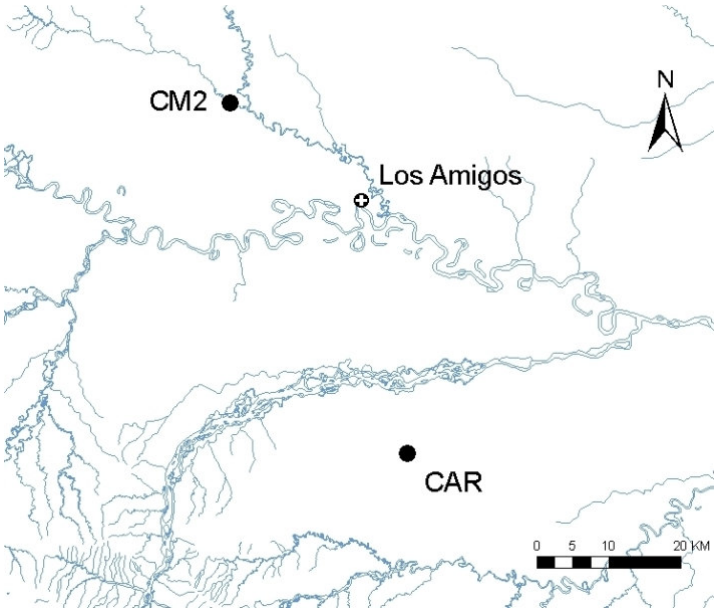

Fig. 2. Additional *A. ararauna* individuals were tagged from two other breeding sites north (CM2) and south (CAR) of the initial breeding site (Los Amigos) to monitor seasonal movements during the dry season.

Individuals were relocated continually throughout the year for a period of 3 years. Relocation data were obtained via ground-tracking, fixed-station triangulations, and aerial tracking. When an individual was visually located, its position was marked with a GPS, and habitat and behavior were recorded. When visual observation of the individual was not possible, ground-trackers took several bearings from different locations to triangulate the position of the individual. Trackers also took bearings from fixed-stations of known coordinates to triangulate or biangulate the position of each individual. Positions of individuals located during over-flights were recorded with a GPS and later downloaded with OziExplorer (Brisbane, Australia) and edited using flight notes and track data. All data were recorded in field-notebooks, and then entered into Excel (Microsoft Corporation) databases for processing and further analysis.

Sampling intensity of relocations varied by season and site. At Los Amigos, sampling intensity during breeding season was an average of one relocation/week/individual. During non-breeding season sampling intensity at Los Amigos remained the same for individuals remaining in their breeding area. As individuals from Los Amigos dispersed, a fixed-wing aircraft was used to relocate them as well as the individuals from the other two sites (CM2 and CAR). Sampling intensity varied according to aircraft availability and other logistical limitations, and generally occurred monthly over a period of 3-5 consecutive days. To minimize spatial autocorrelation during aerial from aerial monitoring, I ensured at least 24 hours between relocations.

Instrumentation

VHF transmitters (model AI-2C) developed for macaws by Holohil Systems (Carp, Ontario, Canada) were within the recommended range of 3% of body weight (Withey et al. 2001). Equipment used for capture included customized traps made of Avinet 127 mm mesh mist nets (Dryden NY), flexible wire, and fishing line.

For tracking, R-1000 portable VHF receivers (Communications Specialists Inc., Orange, CA) were used. Antennas used were 3-element RA-14 Yagi directional antennas, and the RA14K "H" type antennas (Telonics, Mesa, AZ). Two fixed-wing RA-2A (Telonics) antennas were used for over-flights. For fixed-station tracking, large 8-element rotating antennas were installed on tree platforms and towers. Handheld antennas were also used on tree platforms and towers. Handheld GPS 12XL units (Garmin, Olathe, Kansas) were used because of their ability to capture satellites under dense canopy.

Data processing

Processing of locations for home range estimation

Locations obtained by triangulations were processed with LOCATE software (Tatamagouche, Nova Scotia, Canada). The type of estimator used was the Maximum Likelihood Estimator (MLE) which weights all bearings equally, and is recommended when there are less than five bearings for estimated location. Bearing error (angle standard deviation (S.D.)) was not constant due to factors such as: the person taking the bearing, the telemetry system and equipment used, signal bounce due to topographical

differences in the study area, the movement of transmitters as the macaws moved their heads, and variation in weather (Nams 2000). For estimations using three or more bearings, bearing error was calculated independently to generate a 95% error ellipse. To assign a bearing error for locations estimated using biangulations (an error ellipse is not possible when only two lines intersect), field tests of 50 known locations resulted in a bearing error of S.D. = 12, which is conservative considering the default value is S.D. = 2.5. Visual locations marked with a GPS had a location error of approximately 20 meters. Location error obtained by the ultralight airplane was 200 m and for the Cessna it was 500 m. Audio locations had an associated error of 50 m.

Triangulation estimations with location error ellipses in the upper 10% of the dataset were removed (White and Garrot 1990). Upon examination of these locations, it was evident they were poor estimations based on signal strength, topography, and previous signals from other tracking locations. Locations within 50 m of the previous location were removed to reduce autocorrelation (redundancy), based on the observation that macaws often leave the original tree to a neighboring tree (50 meters in closed canopy) when alarmed, rendering the second point dependent on the first point because of its proximity. For space use analyses, the locations were organized by species and individual, pooled across years, and each dataset was split into 2 seasons: 1) breeding season which ranged from Oct 01st to April 30th, and 2) non-breeding season which ranged from May 01st to September 30th. For the landscape analyses, dry season (non-breeding season) individuals of *A. ararauna* were pooled across three different sites (Table 1).

Table 1
Number of individuals and locations (n) in each dataset for the different space use analyses (home range estimation, overlap, dispersion), and landscape analyses (habitat selection, non-random habitat use, and patch analysis). (LA = Los Amigos, A = Adult, J = Juvenile).

	Space Use					*Landscape analysis*		
Species	AA	AC	AM	AC	ACnb	AA	AA	AA
Site	LA	LA	LA	LA	LA	LA	CM2	CAR
Capture	nest	nest	nest	cavity	lick	nest	nest	nest
Total captured	15A,2J	7	8	3	15	15	8A,1J	7A,1J
Independent	13A,1J	5	6	3	15	14	5	7
Breeding season	8(455)	3(225)	3(114)	-	4(96)	-	-	-
Non-breeding season	11(664)*	3(255)	3(187)	-	4(56)	15(722)	9(41)	7(40)
Annual	12(1286)	3(480)	3(301)	-	-	-	-	-

*For space use comparison of *A. ararauna* between seasons, the same 8 individuals were used for the analysis, with a total of 549 locations (8(549)).

Because home range estimation is based on the statistical distribution of fixes (relocations) of animals (Harris et al. 1990), there are several statistical and biological considerations when estimating and analyzing home ranges. Serial autocorrelation of points, whether a home range exists (site fidelity) and minimum sample size (area asymptotes), are three issues which are related but often neglected (Laver and Kelly 2008). I explored each of these issues to assess their effect on home range estimation prior to calculating home range sizes.

Tests of independence

Serial autocorrelation in location data can be problematic for estimating home ranges because most analyses assume all location data are independent. If the location of an animal depends on its previous location, the final dataset will contain redundant data (Swihart and Slade 1985) and introduce bias to home range estimation. I tested for independence of temporally ordered sets of n bivariate locational data (X_i, Y_i,) of 8 individuals of *A. ararauna* using The Home Ranger software (Hovey 1999), which uses

Schoener's ratio t^2/r^2 (Schoener 1981). In this ratio, t^2 represents the mean squared distance between successive observations, and r^2 is the mean squared distance from the center of activity (Swihart and Slade 1985), m represents the number of pairs of successive observations, $\bar{X} = \sum X_i/n$ and $\bar{Y} = \sum Y_i/n$, and:

$$t^2 = \frac{1}{m}\sum_{i=1}^{m}(X_{i+1} - X_i)^2 + \frac{1}{m}\sum_{i=1}^{m}(Y_{i+1} - Y_i)^2,$$

$$t^2 = \frac{1}{m}\sum_{i=1}^{m}(X_{i+1} - X_i)^2 + \frac{1}{m}\sum_{i=1}^{m}(Y_{i+1} - Y_i)^2,$$

and,

$$r^2 = \frac{1}{(n-1)}\sum_{i=1}^{n}(X_{i+1} - \bar{X})^2 + \frac{1}{(n-1)}\sum_{i=1}^{n}(Y_i - \bar{Y})^2.$$

Of the 8 datasets tested for statistical independence, 5 individuals had location data that was significantly autocorrelated (Table 2).

Table 2
Data sets tested for statistical independence after manual removal of locations (n) separated by an interval of < 10 minutes and distance of < 50 meters did not reduce the amount of serial autocorrelation.

Name	*n*	*Schoener**	*Swihart-Slade***
bravo	57	**1.29269**	**0.79614**
diana	51	1.88393	0.39769
houdini	95	**1.34404**	**0.94249**
inti	38	**1.15977**	0.35304
jessi	34	1.62567	0.59736
mary	129	**1.37757**	**0.86652**
oasis	41	**1.34362**	**0.70081**
puente	75	1.63451	0.55125

* values < 1.6 and > 2.4 indicate **significant autocorrelation**
values > 0.6 indicate **significant autocorrelation

Autocorrelation can be reduced by determining the smallest time interval which allows a nonsignificant ratio to be followed by two additional nonsignificant ratios (Swihart and Slade 1985, 1997). Calculating the time interval necessary to reach statistical independence (TTSI) (Swihart and Slade 1985; Swihart et al. 1988; Swihart and Slade 1997) allows manual removal of locations with time intervals smaller than the TTSI value.

The TTSI and the effect of autocorrelation on home range estimation were first assessed for one individual. Locations from the original dataset (n = 57) were removed to create datasets consisting of locations separated by the hourly time intervals of 1, 2, 3, 4, 6, 7, 8 hrs and daily intervals of 2 and 7 days (Table 3). Some studies report time lags greater than 7 days to reach statistical independence (McNay et al. 1994) which justified testing time lags up to a week. The remaining sample size for each dataset was recorded (n), and the bandwidth (h), which is necessary for kernel home range estimation, was computed by two common methods (LSCV and REF) and recorded for each dataset. Finally, the ratio t^2/r^2 was calculated for each dataset. Statistical significance was achieved when locations were 5 hours apart. However, removal of location points resulted in a reduction of sample size by 30%, which subsequently resulted in inflated bandwidths (h).

Table 3
The TTSI (time to statistical independence) for one individual tested (bravo) was 5 hours, however bandwidth (hLSCV and hREF) increased as sample size decreased which would result in greater smoothing and ultimately an overestimation of home range size.

Time interval	*n*	*Schoener **	*hLSCV*	*hREF*
original data set	57	**1.29269**	97.5	583.86
every 15 minutes	53	**1.32616**	90.05	610.48
every half hour	53	**1.31091**	96.17	611.6
hourly	47	**1.42266**	156.55	638.97
every 2 hours	45	**1.46845**	157.42	642.54
every 3 hours	43	**1.49947**	191.14	650.67
every 4 hours	40	**1.54333**	288.54	670.64
every 5 hours	38	1.64936	446.8	672.63
every 6 hours	38	1.64936	446.8	672.63
every 7 hours	38	1.64936	446.8	672.63
every 8 hours	38	1.64936	446.8	672.63
every 2 days	33	1.64324	452.78	671.78
every 7 days	24	1.63853	551.72	784.52

* values < 1.6 and > 2.4 indicate **significant autocorrelation**

When the home range of this individual was estimated using the different lag times and two methods of bandwidth selection (hREF and hLSCV), the non-autocorrelated locations generated home ranges that were 1000 and 1500 ha larger than the data set containing all locations (Fig. 3). Intuitively, a home range should be more accurate by increasing the number of observations of an animal, thereby achieving a more representative sample of its entire range of movements, not by removing observations.

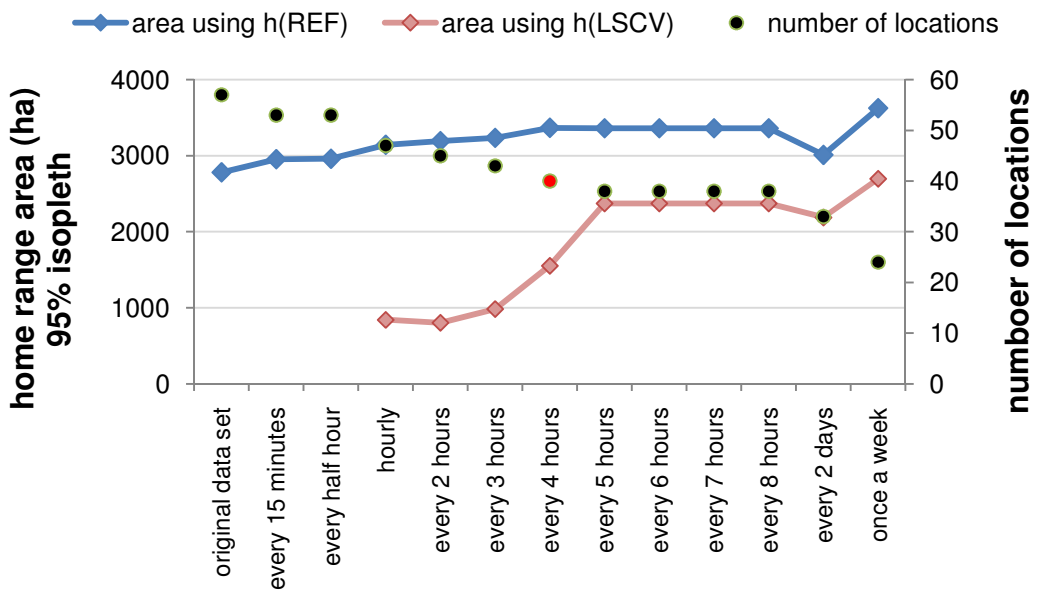

Fig. 3. The amount of autocorrelation decreased as autocorrelated points were removed from each dataset, but as a result the home range size was overestimated. The home ranges for each dataset containing different levels of autocorrelation were estimated (using the REF and LSCV options for bandwidth) and plotted against the number of locations used to generate each home range. The original dataset of 57 locations was autocorrelated until a dataset containing only location points ever 4 hours was obtained (red point).

Although it is important to consider serial autocorrelation (Laver and Kelly 2008), the degree of influence on home range estimation is much debated. As was demonstrated above, achieving statistical independence inflated the bandwidth which would subsequently generate a gross over estimation of home range. Accuracy of home range estimation is significantly influenced by the choice of bandwidth (Park and Marron 1990; Sheather and Jones 1991; Jones et al. 1996; Loader 1999; Gitzen and Millspaugh 2003; Gitzen et al. 2006; Jin and Xueren 2009), sample size and comparatively little by the amount of autocorrelation (Hart and Vieu 1990; Reynolds and

Laundre 1990; Hall et al. 1995; Vilar and Vilar 2000; Fieberg 2007) and the length of time it would take to achieve a minimum sample size may not be feasible (Fieberg 2007). Furthermore, by sampling at longer intervals, biological information is sacrificed at the expense of achieving statistical independence (Reynolds and Laundre 1990; McNay et al. 1994; Solla et al. 1999). Autocorrelation presented itself as an issue with the advent of GPS tracking systems, but this study does not have data-rich location data.

Ultimately, one must consider the objectives of the study and collect data that best represents the biological traits of the animal (Kernohan et al. 2001). A thorough review of home range studies prompted Laver and Kelly (2008) to recommend that the time to biological independence (TTBI) be reported as well. Unlike the TTSI, the TTBI considers the mobility of the animal, and is attained when sufficient time is allowed between observations so that the animal can relocate to any point within its home range home range (Lair 1987; McNay et al. 1994; Swihart and Slade 1997; Kernohan et al. 2001). Macaws fly roughly 50 km/hour, which means if the longest distance from one end of the range to the other is 10 km; the TTBI would be approximately 10 minutes.

If statistically autocorrelated data were truly a problem whereby macaws would not have sufficient time to appear anywhere within their range, one would expect that short sampling intervals would be correlated with smaller distances between locations, and long sampling intervals would be correlated with larger distances between locations. However, this is clearly not the case as can be seen in (Fig. 4). In this later analysis, breeding season data of 6 individuals were compiled and distances between consecutive

locations were plotted against the time interval between locations (n = 418), and there was no significant correlation between time and distance (p = 0.192).

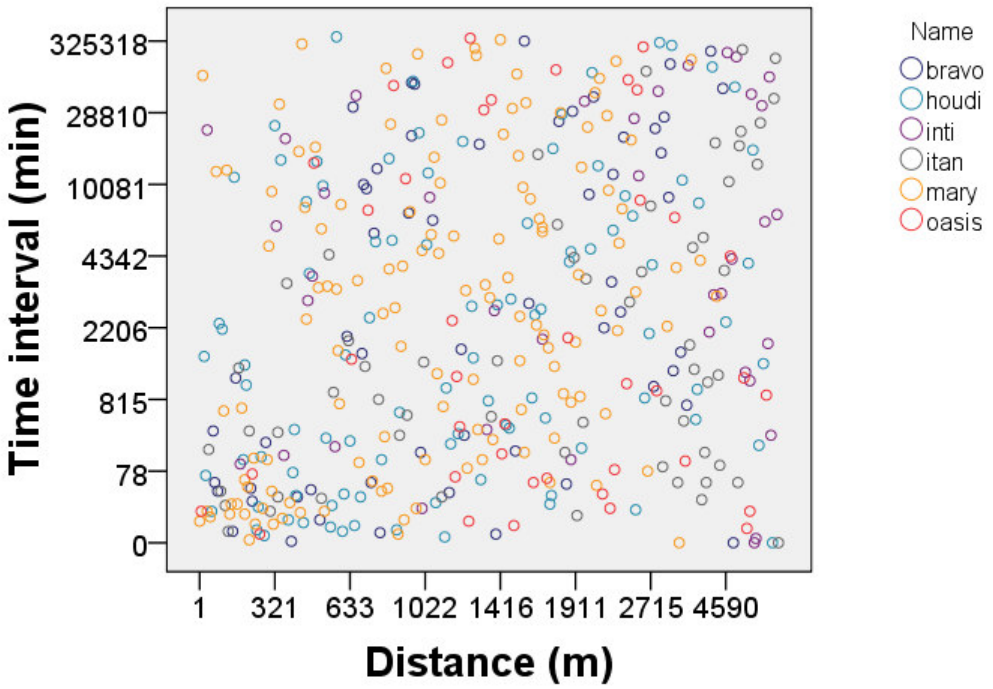

Fig. 4. Distances between consecutive macaw locations were plotted against the time intervals separating each location (n = 418), and there was no significant correlation between time allowed between locations and distance moved by macaws (p = 0.192), demonstrating that autocorrelation within the data sets was not enough to bias the results.

Although I did not determine the influence of autocorrelated data during the dry season when movements extend far beyond the breeding area, sampling intervals were greater than 24 hours. This would allow: 12 hours (daylight hours) x 50 km/hr = 600 km distance between locations which is well beyond the distance macaws have been located. Thus, macaws would have sufficient time to appear anywhere within their range. Testing

for statistical independence for the purpose of removing location points to achieve statistical independence does not justify the loss of biological information that would occur as a result of this. In lieu of the relative unimportance that autocorrelation has on final home range estimation, I did not determine the TTSI for other individuals, but instead elected to preserve the sample size and associated biological information.

Assessing site fidelity

Before any home range analysis is performed, it should be established whether a home range exists. Several definitions of home range have been used (Burt 1943; Worton 1987; White and Garrot 1990) however they do not provide a quantitative way to test their existence, thus are not "operational" (Spencer et al. 1990). Site fidelity can be analyzed to distinguish between three general types of movements: migration, dispersal, and localized movement (Kernohan et al. 2001). If a home range exists, it follows that site fidelity exists. Site fidelity "exists when the observed area used by an individual is significantly smaller than the area used if an individual's movement was random" (Munger 1984; Danielson and Swihart 1987), and since site fidelity can be measured, so can the existence of the home range (Spencer et al. 1990).

To determine whether fixes exhibited site fidelity (constitute a home range), I used the procedure modified by (Danielson and Swihart 1987) which compares observed fixes of an individual with randomly generated fixes. The Animal Movement extension (Hooge and Eichenlaub 1997) was used to calculate site fidelity for each individual for each season in ArcView GIS 3.2a (ESRI 2000). This procedure calculates the distances between successive fixes of the actual dataset, and associates each selected distance with

an associated randomly generated bearing angle. The resulting X, Y coordinates of the random locations generates a random movement path. A Monte Carlo simulation was used to determine if observed movement pattern has more site fidelity than should occur randomly. This procedure was repeated to yield 100 random movement paths per individual per sampling period.

As expected, during the breeding season, the observed movements were more constrained than random movement paths, thus site fidelity existed for all breeding individuals (Table 4). During non-breeding season, site fidelity varied: 6 of eleven *A. ararauna* (AA), 1 of 3 *A. chloropterus* (AC), and 3 of 3 individuals of *A. macao* (AM) exhibited site fidelity. Although some individuals lacked site fidelity during the non-breeding season, true site fidelity actually existed because each individual returned to the breeding area on several occasions throughout the season, and returned for breeding season. Based on this outcome, home ranges were estimated for individuals captured from nests. Home ranges were not estimated for *A. chloropterus* that were tagged at the clay lick, due to lack of fidelity demonstrated by their disappearance from the monitoring area.

Table 4
Site fidelity was exhibited by all breeding individuals during the breeding season. During the non-breeding season, more than half of the marked population of *A. ararauna* lacked site fidelity, however true site fidelity did exist as all individuals seasonally returned to their nesting site.

	Breeding season			*Non-breeding Season*		
Species	n	Site fidelity	No site fidelity	n	Site fidelity	No site fidelity
AA	10	10	0	11	5	6
AM	3	3	0	3	3	0
ACbr	3	3	0	3	2	1

Minimum sample size

Whether sample sizes are large enough to be representative of the home range of an animal is another consideration when performing a home range analysis. The often-cited minimum sample size of 30 to 50 locations is derived from studies based on simulation data (Seaman et al. 1999). However, empirical studies report anywhere from 23 to over 200 locations as minimum sample sizes (Laundre and Keller 1984; Gese et al. 1990; Harris et al. 1990), thus it is clear that minimum sample size varies with the animal of study, statistical distribution of locations, spatial pattern of location points, and method of estimation.

Ideally, determining minimum sample size should be based on the number of locations needed for the range size to stabilize (Swihart and Slade 1985; Harris et al. 1990; Seaman et al. 1999). When home range size is plotted against the number of locations (Gese et al. 1990), an asymptote should be obtained if the range does not contract or expand (Harris et al. 1990), site fidelity exists (Gautestad and Mysterud 1995), and sampling time is sufficient to capture the full range of movements (Bowen 1982). The point at which addition of more locations does not change the home range size is the desired minimum sample size.

Several area-observation curves were generated for data-rich individuals, yet as locations were added over time, clearly defined asymptotes were rarely obtained even though sample size and time were sufficient to represent the range. Only two area-observation curves were successful in revealing an asymptote. When the home ranges of random subsets of 10, 20, 30, etc. locations for two individuals were plotted (Fig. 5), the

95% home range area changed very little once the sample size was greater than 20, indicating that for these two individuals, the minimum sample size was 20 locations for home range estimation. However, considerations other than relying on clearly defined asymptotes as the sole criterion were explored for determining whether a home range should be estimated.

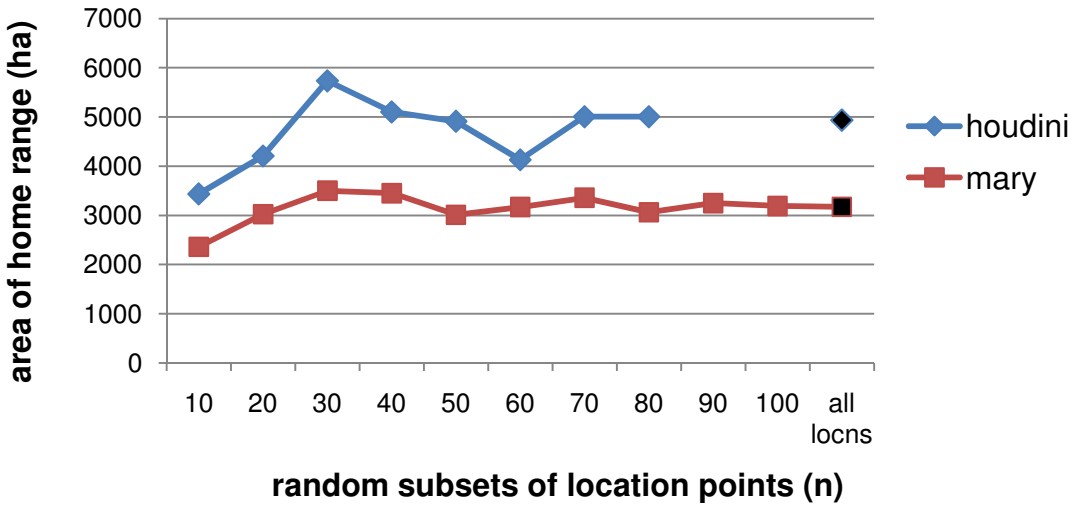

Fig. 5. Home range changed very little once the sample size was greater than 20 when random subsets of different sample sizes for two individuals were plotted against their corresponding home range size. Once a sample size of 25 locations was reached, the home range size was equal to home range size estimated using all location data (black points).

After failing to obtain clearly defined asymptotes for all but two individuals, it was concluded best to examine each dataset individually and use prior knowledge of the individual for deciding whether it would be included in the home range estimation (Laver and Kelly 2008). Area-observation curves do not consider the biology of the

animal (Kernohan et al. 2001), or the influence of sample size and sampling interval (Hansteen et al. 1997; Otis and White 1999; Kernohan et al. 2001). Biological sample size, defined as the number of locations that are "representative of the movements and activities exhibited over the study period (Kernohan et al., 2001) varies by individual, as does statistical sample size. Failure to achieve an asymptote to determine statistical sample size was not a suitable method to include or exclude individuals for home range analysis, thus in accordance with considering prior knowledge of the animal, other criteria were developed.

Criteria for determining datasets used for estimating home range

Seasonal home ranges were only estimated for individuals that had at least one full season of data, and total ranges were estimated only for individuals that had a least one full year of data. It was already established by site fidelity tests that only nesting individuals had site fidelity. Prior knowledge of the behavior of *A. chloropterus* captured at the clay lick confirmed that home range estimation for these individuals was not appropriate. For all other individuals, I used a minimum sample size of 20 locations per individual per season as a primary criterion for selecting individuals for home range estimation. However, this value may not apply to all individuals equally, and since it was not possible to determine the minimum sample size on a per individual basis, I used a secondary criteria based on sampling time. If sample size was relatively small, yet the size and location of area used was repeated from season to season, the individual was included. Although these criteria significantly reduced the number of individuals for

which home ranges could be estimated, the data were still valuable for other analyses (Table 5).

Table 5
Final datasets for analysis of space use (home ranges, overlap, and dispersion). Seasonal ranges were estimated from all individuals that satisfied the criteria for home range calculation, but comparison of how range sizes differ between seasons required that the same individuals from season to season to be used in the analysis, excluding 3 individuals of *A. ararauna* which did not have both seasons of data.

Comparison	*Season*	*AA*	*AC*	*AM*
Within season	Wet	8 (455)	3 (225)	3 (114)
	Dry	11(664)	3 (255)	3 (187)
Between seasons	Wet	8 (455)	3 (225)	3 (114)
	Dry	8 (549)	3 (255)	3 (187)

Processing of habitat attributes for habitat and landscape analysis

Habitat attributes were extracted from a land cover layer that was created using a Geographic Information System (GIS) (ArcMap 9.2, ESRI 2006) (Fig. 6). This layer was developed from a combination of remotely sensed images (Landsat 7 ETM+), ground-level field data and aerial observations, and shapefiles of geology (INGEMMET 2007), geomorphology, physiology, vegetation types and land use (INRENA 2001).

An unsupervised classified image of the larger region (Killeen 2009) with 27 classes provided a base from which to clip the study area, which excluded the mountainous region of the Andes which are unsuitable habitat for macaws. It also provided several land cover types that were not included in the shapefile layers. A 30 x 30 m resolution ML supervised classified map was created using ENVI software (ENVI

2008) from a Landsat 7 ETM+ image (July 2000) and used to identify palm swamp habitat (see Appendix B for detailed methods). It consisted of 15 land cover classes (pair separability = >1.85, overall accuracy = 61.43%, Kappa Coefficient = 0.5867) of which 4 were wetland types (accuracy 87.7%). The final image was smoothed using a majority analysis with a kernel size of 3 x 3 pixels.

Shapefiles were edited to include land use such as agricultural fields, mining sites, and plantations that were displayed from both classified images. Palm swamps from the shapefiles were cross-checked with the supervised classified image and edited. The attributes of each shapefile were edited to ensure consistency of names and descriptions among files, and merged to create a single land cover layer that included the original data associated with each file (geology, geomorphology, physiology, and vegetation type, information on habitat type, and soil type). The final layer with multiple attributes for each geographic point was used for the habitat selection analysis and a DEM (Tobler 2000) was used as a separate layer to extract elevation data. For the landscape analysis (Patch Analysis and non-random use of palm habitat) attributes were dissolved so that only a single attribute existed at any geographic location.

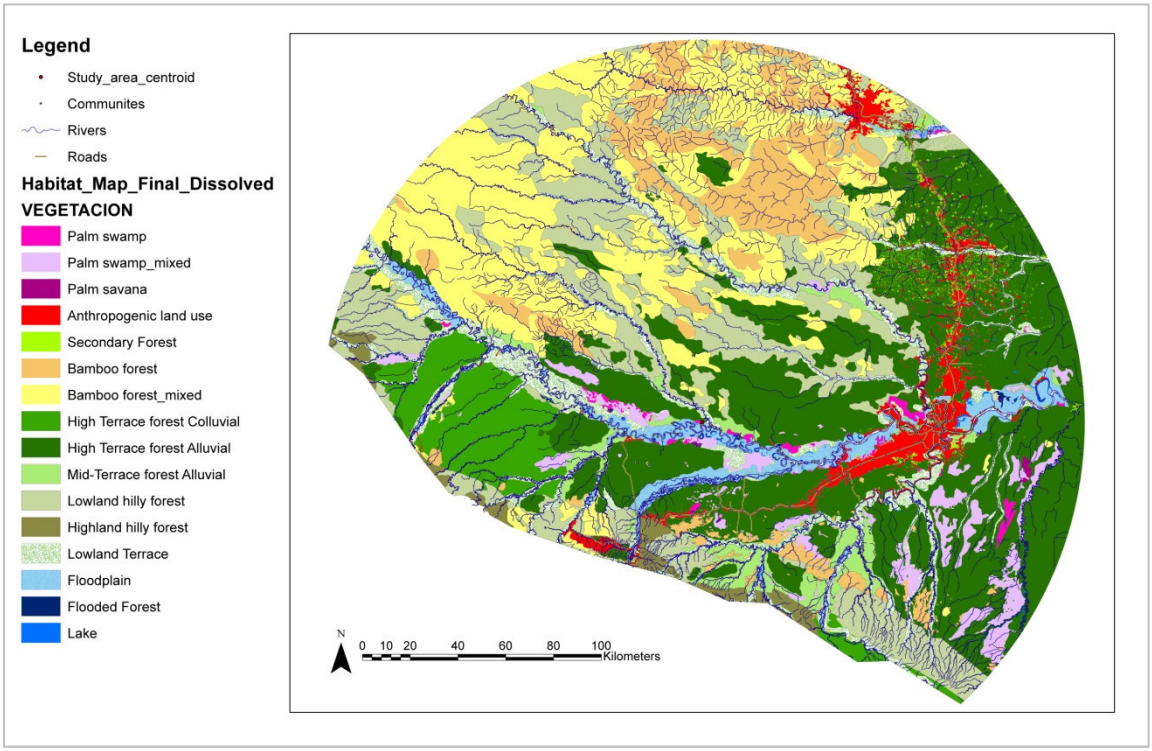

Fig. 6. Land cover map of the study area for use in habitat selection and landscape analysis.

Processing of resource units for habitat and landscape analysis

Three types of analyses were performed to examine habitat use by *A. ararauna* during the dry season, which required different definitions of resource "use" and "availability", as well as different spatial extents that were sampled (Table 6). To determine whether habitat selection existed (if macaws were using certain habitats at a greater proportion than the proportion occurring in the environment), sampling protocol A (SP-A) was used (Manly et al. 1992) which compares "used" resource units with "available" resource units. Sampling protocol for examining non-random proximity to palm habitat also falls under SP-A, and comparison of the landscape used by macaws

with areas where they were not observed (Patch Analysis) represents SP-C which compares "used" and "not-used" resource units.

Table 6
Definition of sampling extent, resource units, and sampling protocol (SP) and design for the three habitat and landscape analyses to describe dry season habitat use by *A. ararauna*.

Definition	*Habitat Selection*	*Proximity to wetlands*	*Patch Analysis*
Used resource units	macaw locations (n = 803)	macaw locations (n = 803)	Habitat patches censussed within "used" extent defined by macaw locations
Available/unused resource units	Available units randomly sampled throughout study area (n = 803)	Available units randomly sampled throughout study area (n = 803)	Habitat patches censussed from "not-used" area
SP and Design	SP-A/Design II	SP-A/Design II	SP-C/Design II

For all analyses, habitat within the range of radio-telemetry locations was compared to habitat throughout the entire study area, which falls under Design II (Johnson 1980) as outlined by Thomas and Taylor (1990). Design II measures "used" resources for marked individuals and "available" or "not-used" resources at the population level (Thomas and Taylor 2006). This allowed for telemetry locations of individuals to be pooled across years (Manly et al. 1993) to maintain sufficient sample size. Dry season locations ("used" resource units) of all marked individuals of *A. ararauna* from Los Amigos, CM2, and CAR were pooled across years (n = 803 locations). Of the 16 individuals from Los Amigos, two were related (parent/offspring), so only locations of the offspring that were different from the parent locations were included to avoid redundancy.

For the habitat selection and non-random proximity to palm habitat analyses, the "used" resource units were location points of macaws themselves, and for the patch analysis, the "used" resource unit was an area defined by a 10 km buffer around the range of macaw locations which was censussed (Fig. 7). Available resource units for habitat selection and non-random habitat use were sampled (n = 803) throughout the study area using the random sample generator in Hawth's Tools (Beyer 2004). For the patch analysis, the "not-used" area of the landscape was censussed.

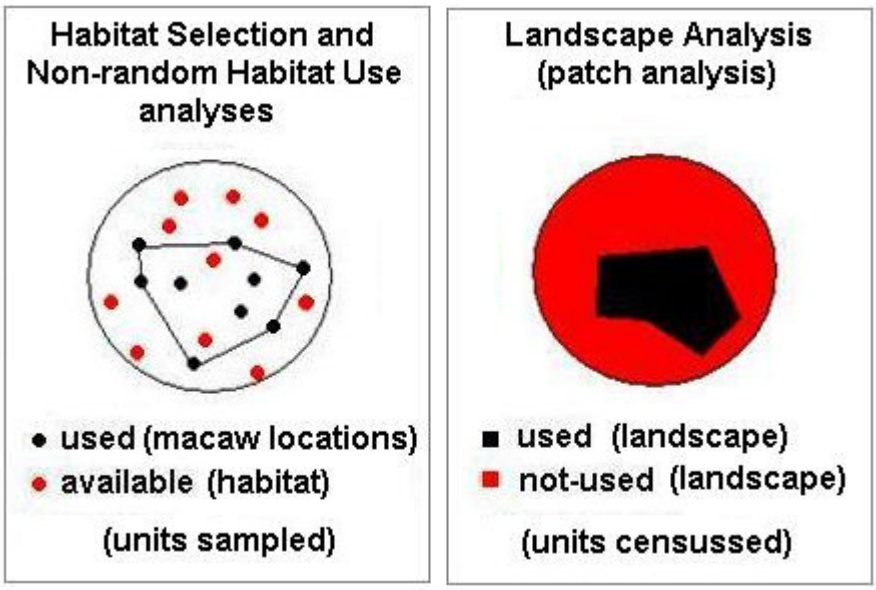

Fig. 7. Sampling units and spatial extents used for habitat selection, non-random proximity to palm habitat analysis (left) and landscape analysis (right).

The spatial extent from where the "available" and "not-used" resource units were sampled was determined by the distribution of relocation points of radio-marked macaws

(McClean et al. 1998) and delimited by single circular plot with a radius equal to the furthest relocation point (160 km). It was assumed that all individuals were able to fly the distance of the furthest point. Due to the mobility of macaws and lack of topographical barriers within the spatial extent used, availability is assumed to be equal for all individuals, meaning that all macaws have equal access to all resource units.

Data analysis

Home range estimation

Home ranges are a fundamental measurement of wildlife space-use patterns (Hemson et al. 2005), and because they are so critical for management, efforts to improve the accuracy for estimating them still continue (Downs and Horner 2007). Home range estimation is essentially computing the area an animal occupies by delineating the boundary of the home range from sample point locations (Amstrup et al. 2004). Home range estimators should be accurate (low bias, high precision) (Boulanger and White 1990), and stable across samples (Downs and Horner 2009).

Several home range estimators exist. The Minimum Convex Polygon (MCP) (Mohr 1947) is easy to construct, yet has a tendency to over-estimate home ranges due to its sensitivity to outliers, and provides no measure of internal space use (assumes uniform area use) (Worton 1987, 1989). However, this method is still commonly used, easily repeatable and useful for comparison with other studies (Harris et al. 1990; Aarts et al. 2008). MCP's may better represent the total area used by an animal, and are often used when sample size for kernel estimation is believed to be too small. Because the

resulting polygon can contain large areas of unoccupied space, Laver suggests the resulting range should be called a "Total Range" instead of Home Range as it shows the entire area used by that animal (Laver 2005). Total range use is a valuable piece of information, but caution should be made when compared across studies since sample size, sampling duration and treatment of outliers for each individual may be mismatched between studies (Laver 2005).

Kernel density estimators (KDE) are most common (Kernohan et al. 2001) and generate a continuous surface of an animal's utilization distribution by smoothing the point patterns of animal locations (Silverman 1986; Worton 1987, 1989). KDE's are considered to be the best non-parametric choice for individuals that have site fidelity (such as nests) and multiple centers of activity (nests, clay licks, and roosting areas). In addition, this estimator is less sensitive to small sample sizes and doesn't assume a particular statistical distribution (White and Garrot 1990). However, KDE's overestimate when the distribution is not bivariate which is the case for most animal distributions (Blundell et al. 2001), have sharp edges (Getz and Wilmers 2004), or contain large amounts of empty space within their interior (Getz and Wilmers 2004; Hemson et al. 2005; Row and Blouin-Demeres 2006). The amount of smoothing is sensitive to bandwidth (Downs and Horner 2007) and can result in both overestimates and underestimates (Kernohan et al. 2001). Variable results of accuracy can be attributed to lack of robustness to point pattern shape (Blundell et al. 2001; Getz and Wilmers 2004; Hemson et al. 2005; Downs and Horner 2009). In one study that examined the

performance of MCP and KDE on 4 point pattern shapes, the MCP performed best overall (Downs and Horner 2009).

MCP and KDE estimators can be valuable tools for space use analysis, as each can answer different questions; MCP provides a measure of total area used, whereas KDE provide a measure of intensity of use. For this reason, I used both MCP and kernel density estimators (KDE) for home range estimation.

For generating the Minimum Convex Polygon (MCP) I used Hawth's Analysis Tools 3.27 (Beyer 2004), and for the kernel density estimator (KDE) I used HRT for Arcview (Rodgers et al. 2005) with ArcGIS 9.2 (ESRI 2006). The data sets had already been processed to remove bian-gulated or triangulated locations with large associated error, as well as questionable outliers. I used a 100% MCP for each individual home range, as a 95% MCP would have excluded valid outlying points obtained by visual observation and aerial tracking, and would have underestimated the total area used. For the KDE, I used a fixed kernel instead of an adaptive kernel because adaptive kernels over-smoothed outlying areas of the range, incorrectly extending utilized area beyond what was likely used, Moreover, estimates based on adaptive kernel methods are problematic when territoriality exists. The raster cell size was set at 100 m, and I used the extent of the breeding area and non-breeding area. A 95% utilization distribution (UD) was used to calculate the home range area in hectares (Powell 2000). A 99% isopleth for each home range was also generated. I did not scale to unit variance.

Several sources (Silverman 1986; Worton 1987) cite that the kernel estimator used will have little effect on the outcome of the analysis, but the nature of the kernel

(fixed versus adaptive), and the smoothing factor (h) will greatly influence results (Silverman 1986). There are several options for selecting bandwidth. The LSCV-KDE (least-squares cross-validation) failed frequently. The HREF, which is the default reference bandwidth that assumes a Gaussian unimodal distribution (Silverman 1986) oversmoothed as reported in other studies. The LCV (likelihood cross-validation) performed better than the LSCV (Gitzen et al. 2006; Horne and Garton 2006) but it failed more than 50% of the time, as did the BCV (biased cross-validation) smoothing method. Proportions of the HREF have served as a compromise for bandwidth selection (Carr and Rodgers 1998), however when some individuals had inflated bandwidths, using the same proportion for individuals with small bandwidths resulted in extreme undersmoothing or failure of the estimator. As was concluded in other field studies, the final choice of bandwidth was determined by knowledge of the study species and site (Tobler 2008; Palminteri 2010). After a thorough analysis, a bandwidth of 1500 meters was used across all species and individuals for all seasons.

Interspecific and intraspecific seasonal differences of home range size

I tested for differences among home ranges for each species and each season, as well as for differences among species. To test for differences in home range size among the three species a non-parametric Kruskal-Wallis Test was performed, once for breeding season, and again for non-breeding season. To test whether there was a difference in home ranges between seasons, I used the Wilcoxon Signed Ranks Test for related variables (home ranges were related between seasons because the same individuals were compared from one season to the next).

Home range overlap

Home range overlap of nesting macaws during breeding season was quantified using three joint-space use techniques. Each space-use measure can provide a unique estimate of overlap (Millspaugh et al. 2004) thus it's advised against using a single measure of overlap. Even within a single study, using a single measure can generate inconsistent results (Millspaugh et al. 2004) as each technique responds differently to different types of space use patterns.

The home range polygons generated from the MCP estimators were overlapped in GIS and the amount of area shared between individuals was calculated with Hawth's Tools (Beyer 2004) using the Polygon in Polygon Analysis. This two-dimensional technique assumes uniform use within the home range and shared space (Kertson and Marzluff 2009).

The other two techniques are based on 3-dimensional overlap, which assumes unequal use within the home range and are generated from kernel-based utilization distributions. (Fieberg and Kochanny 2005) provide a review of the common overlap indices and recommend Bhatacharyya's affinity index (BA) for measuring the similarity between UD estimates (Bhattacharyya 1943), and the utilization distribution overlap index (UDOI) measuring space-use sharing (Fieberg and Kochanny 2005). These indices range from 0 (no overlap) to 1 (complete overlap) if the UD's are uniformly distributed, but UDOI can be greater than 1 if the two UD's are not uniformly distributed. The formulae are as follows:

$$BA = \iint_{-\infty-\infty}^{\infty\ \infty} \sqrt{\widehat{UD}_1(x,y)} \times \sqrt{\widehat{UD}_2(x,y)dxdy}$$

$$UDOI = A_{1,2} \iint_{-\infty-\infty}^{\infty\infty} \widehat{UD}_1(x,y) \times \widehat{UD}_2\,(x,y)dxdy$$

These two indices were calculated following methodology used by (Kertson and Marzluff 2009).

Each raster layer was converted from a kernel density estimate (values of cells do not sum to 1) to a true probability density function (sums to 1) using the Raster Calculator within Spatial Analyst. This generated a new raster of minimum use for each individual. Using Hawth's tools (Beyer 2004), a point grid was generated to extract the raster value from the middle of each cell. Final calculation of UDOI and BA indices were not possible within ArcMap (ESRI 2006) environment, thus the resulting table of minimum use values for each individual was exported for use in SPSS (SPSS 2007). To calculate the UDOI between 2 individual ranges, the values of each overlapping cell are multiplied. The products are then summed, and the sum is multiplied by the number of cells which contain a value > 0 (a value of 0 indicates there was no overlap for that cell). Each individual was paired with all other individuals, and the resulting UDOI's were then averaged to give an overall value for breeding individuals of that species. The BA was calculated in a similar manner. The values of each overlapping cell were first multiplied then the square root was taken. These values were then summed to give the final BA index of overlap for that pair of individuals. BA's were averaged for each species as was done with the UDOI indices of overlap.

Distance measures

To obtain a measure of dispersion around a center of activity (nest or clay lick), the mean distance from location points to the centre of activity (MDC) was calculated for each individual (AA = 8, AC = 3, AM = 3, ACnb = 4) for each season. In this analysis, non-breeding *A. chloropterus* (ACnb) were included because dispersion measures are not bounded ranges delimiting a territory. For each species and season, the MDC was averaged among individuals (AA = 8, ACbr = 3, AM = 3, ACnb = 4). A non-parametric Kruskal Wallis test was used to test for interspecific differences in MDC during breeding season, and also for non-breeding season. To test whether dispersion between seasons was different, I used the non-parametric Wilcoxon Signed Ranks test for paired related samples of each species.

Habitat selection

Categorical data generated from counts of resource units (used = marked macaw locations, available = random locations) in each land cover type (habitat, geology, geomorphology, ecozone) were analyzed using the program Resource Selection for Windows (RSW), written by Fred Leban (Leban 1999) with Neu's methodology and Bailey simultaneous confidence intervals for determining significance ($\alpha = 0.05$) among habitat types "preferred" or "avoided". An RSF (resource selection function) was not estimated.

Continuous variable attributes associated with each sample unit (used and available) were expressed as point (at sample point), proximity (distance from the sample point to a feature on the landscape), or area measurements (circular plot centered

on the sample point) (Table 7). These circular buffers of 500 m and 2500 m radius allowed the inclusion of variables of an area-based nature and better match the scale at which animals may be actually selecting (Boyce et al. 2003; Johnson et al. 2004; Boyce 2006). Once the values of each attribute were calculated for all resource units, a paired-sample t-test was used (Wilcoxon Signed Ranks Test) to compare the "used" units of marked individuals with their corresponding "available" units.

Table 7
Habitat attributes for each "used" and "available" resource sample unit (n = 803 of each resource unit type) were measured at multiple scales: at the sample point, as a distance from the sample point, or within a buffered area surrounding the sample point (RSW = Resource Selection for Windows, WSRT = Wilcoxon Signed Ranks Test).

Sample unit	*Attribute*	*Details*	*Test*
Point (categorical)	Habitat type	Palm swamp, mixed palm forest, floodplain, etc	RSW
(categorical)	Ecozone	Humid, very humid, tropical, subtropical, etc	RSW
(categorical)	Geology	Alluvial, colluvial, etc	RSW
(continuous)	Elevation	Ranges 180-570 masl, extracted from DEM	WSRT
Proximity (m)	Distance to features	Roads and communities	WSRT
Plot-based (500m)	Sum of river length	Association with riparian habitat	WSRT
(2500m)	Habitat composition	No. ha of habitat present in each buffered sample	WSRT
(2500m)	Patch richness	Number of different habitat types	WSRT

Non-random proximity to palm habitats

To explore how the distribution of palm habitat may be related to dry season movements of *A. ararauna*, I examined the relationship between the configuration of wetland features across the landscape and the pattern of macaw telemetry locations using Spatial Analysis (ESRI 2006). The proximity of habitats to macaw locations when compared to random locations is indicative of the importance of those habitats to macaws. I measured Euclidean distances between patches of wetlands over the entire

extent of the landscape. Each cell in the resulting matrix had a proximity value based on its distance to the closest wetland. Macaw locations (n = 803) were overlaid with this distance matrix, and the distance values associated with each macaw location were extracted from the distance matrix. Distance values were plotted with the location frequency. To compare the observed spatial pattern of macaw locations with a random pattern of macaw locations, an additional dataset of randomly generated points (n = 803) overlaid on the distance was processed in the same manner. The Mann-Whitney two-independent sample test was used to determine whether the distances to wetlands of macaw locations were significantly different from those of the random points. Differences in proximity between wetland types (pure palm habitat vs. mixed palm habitat) were also examined by generating a frequency distribution of proximity values for each wetland type on the same plot.

Patch analysis

I also explored how overall landscape pattern may influence habitat use by comparing patch attributes of "used" and "not-used" areas of the landscape. Landscape metrics (patch diversity, patch richness, patch density, patch size, and patch evenness) were used to quantify habitat patterns with the "used" area and the "not-used" area using Patch Analyst 0.9.5 (Ontario Ministry of Natural Resources, Canada). The characteristics of "preferred" habitats (as determined by habitat selection analysis) within each landscape type ("used" and "not-used") were compared with the characteristics of the "avoided" habitats.

RESULTS

Home range sizes

Seasonal range

Mean home range size (based on the 95% KDE) during breeding season (Table 8) for each species of macaw (AA, AM, AC) was 7,682 ha ± 1,061 SE, 7,536 ha ± 1,304 SE, and 7,330 ha ± 1,442 SE respectively, and ranging from 4,945 to 14,248 ha (Fig. 8). There was one outlier in the analysis of *A. ararauna*, and when this individual was excluded, the mean home range size for *A. ararauna* during breeding season was 6,739 ha ± 324 SE.

Table 8
Descriptive statistics of mean home range sizes (ha) during the breeding season for each species of macaw (based on the 95% KDE).

Species	*N*	*Mean (ha)*	*Std. Error*	*Range*	*Min*	*Max*	*Std. Dev.*	*Variance*	*Skew-ness*	*SE*
AA	8	*7682.37	1061.37	8707	5541	14248	3002.01	9012070.26	1.85	.75
AM	3	7536.00	1304.06	4145	4945	9090	2258.71	5101783.00	-1.63	1.23
AC	3	7329.67	1442.35	4926	5108	10034	2498.22	6241094.33	.84	1.23

* Excluding the outlier gives a mean home range size of 6739 ha ± 324 SE for *A. ararauna*.

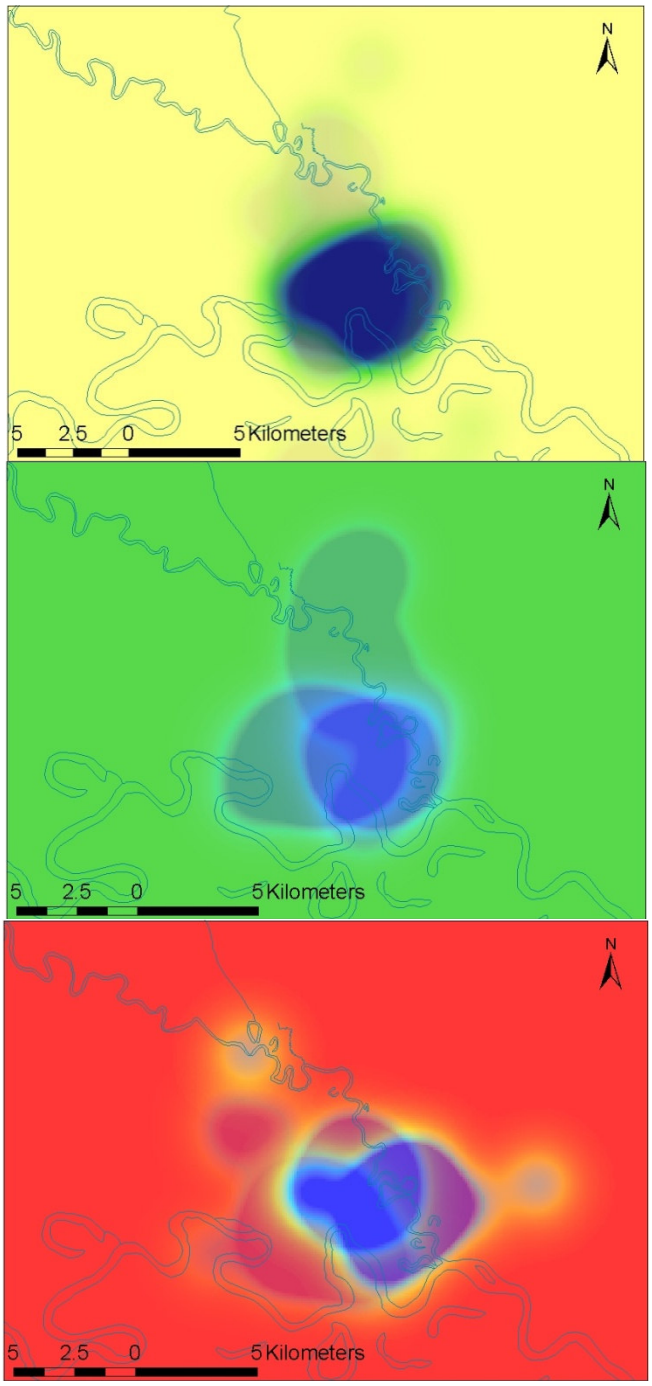

Fig. 8. Breeding season ranges for *A. ararauna*, *A. chloropterus* and *A. macao*. Mean range size was 7,516 ha and there was no significant difference among mean range size among species ($p = 0.350$).

The non-breeding mean range size (based on the 95% KDE) during non-breeding season (Table 9) for *A. ararauna*, *A. macao*, and *A. chloropterus* was 13,171 ha ± 1,215 SE, 15,320 ha ± 6,427 SE, and 8,766 ha ± 1,655 SE respectively, and ranged from 3,769 to 21,542 ha.

Table 9
Descriptive statistics of mean range sizes (ha) during the non-breeding season for each species of macaw (based on the 95% KDE).

Species	*N*	*Mean (ha)*	*Std. Error*	*Range*	*Min*	*Max*	*Std. Dev.*	*Variance*	*Skew-ness*	*SE*
AA	11	13171.20	1214.90	3769	10746	14514	2104.26	4427922.80	-1.70	1.23
AM	3	15320.30	6426.97	21542	6171	27714	11131.83	1.239E8	1.20	1.23
AC	3	8766.20	1655.32	5581	5595	11176	2867.10	8220262.13	-1.11	1.23

Mean range size using the MCP for AA, AM, and AC during breeding season was 2,541 ha ± 690 SE, 2,508 ha ± 993 SE, and 1,540 ha ± 312 SE respectively (Table 10). The non-breeding ranges were 117,849 ha ± 57,654 SE, 49,815 ha ± 28,487 SE, and 12,674 ha ± 7,828 SE respectively (Table 11). The dry season movements of *A. ararauna* were south and east of the breeding range (Fig. 9).

Table 10
Descriptive statistics of mean range sizes (ha) during breeding season for each species of macaw (based on the MCP).

Species	*N*	*Mean (ha)*	*Std. Error*	*Range*	*Min*	*Max*	*Std. Dev.*	*Variance*	*Skew-ness*	*SE*
AA	8	2542	689	4956	986	59421	1950	3804233	1.048	0.75
AM	3	2508	994	3386	635	4021	1721	2963284	-0.901	1.23
AC	3	1541	312	1082	994	2076	541	292778	-0.097	1.23

Table 11
Descriptive statistics of mean range sizes (ha) during non-breeding season for each species of macaw (based on the MCP).

Species	*N*	*Mean (ha)*	*Std. Error*	*Range*	*Min*	*Max*	*Std. Dev.*	*Variance*	*Skew-ness*	*SE*
AA	11	117849	57654	535360	3249	538609	191217	36564058284	1.90	0.66
AM	3	49815	28487	98627	1457	100084	49341	2434566737	0.17	1.23
AC	3	12674	7828	24856	3376	28232	13559	183850450	1.64	1.23

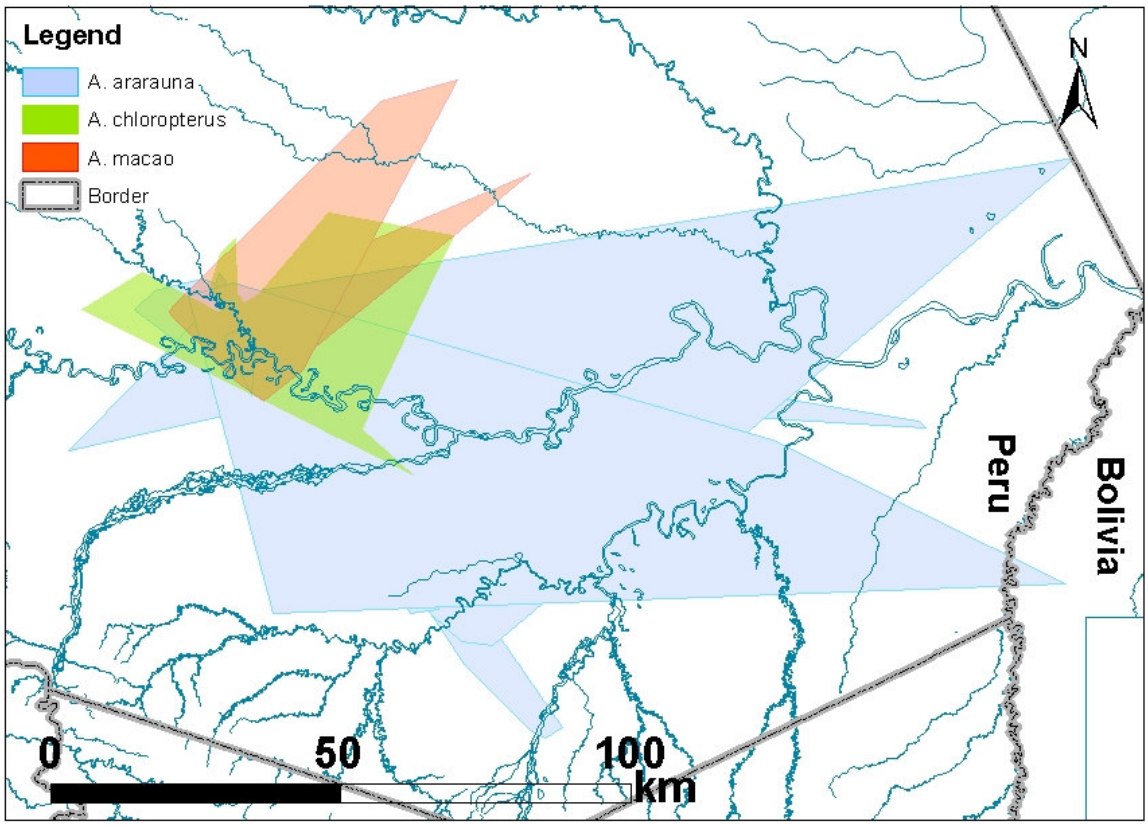

Fig. 9. The dry season movements of *A. ararauna* were south and east of the breeding range. Minimum mean area used was 117,849 ha, but since macaws migrated beyond international borders the full range of movements was not captured.

Total range

Total range, representing all locations throughout the year was generated for all individuals for each species with the MCP estimator (Fig. 10). Mean range size for *A. ararauna* (AA), *A. macao* (AM), and *A. chloropterus* (AC) was 116,907 ha ± 59,513 SE, 6,398 ha ± 4,186 SE, and 20,823 ha ± 15,488 SE respectively (Table 12).

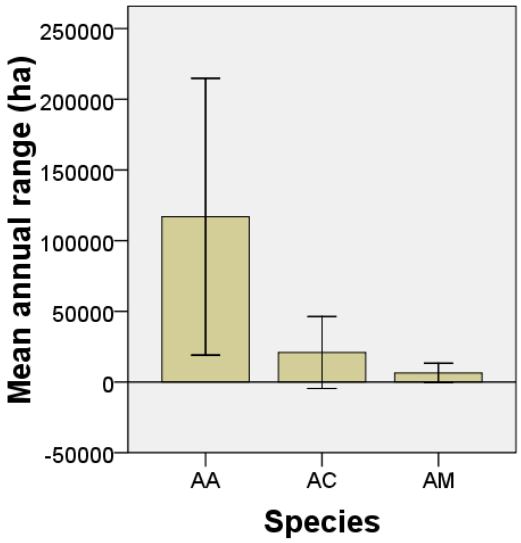

Fig. 10. Mean area (ha) of total ranges for *A. ararauna* (n = 12), *A. chloropterus* (n = 3) and *A. macao* (n = 3) with 95% confidence intervals (based on MCP). Error bars represent a 95% CI for the mean.

Table 12
Descriptive statistics for mean total range for each species estimated using the MCP (AA = *A. ararauna*, AM = A. *macao*, AC = *A. chloropterus*).

Statistic	*Total AA*	*Total AM*	*Total AC*
Mean Range (ha)	116907.25	6398.17	20823.53
Standard Error	59513.14	4185.73	15487.47
Standard Deviation	206159.57	7249.90	26825.09
Sample Variance	42501762546	52560949	719585439
Kurtosis	3.43 ±1.23SE	-	-
Range	626739.45	13902.95	47672.68
Minimum	3928.69	635.25	4091.51
Maximum	630668.14	14538.20	51764.19
Count	12	3	3
Confidence Level (95.0%)	130987.53	18009.73	66637.22

Interspecific differences in range size

Breeding season range sizes (Fig. 11) generated by the KDE for each of the three species of macaws showed no significant difference among mean rank of range sizes ($p = 0.350$).

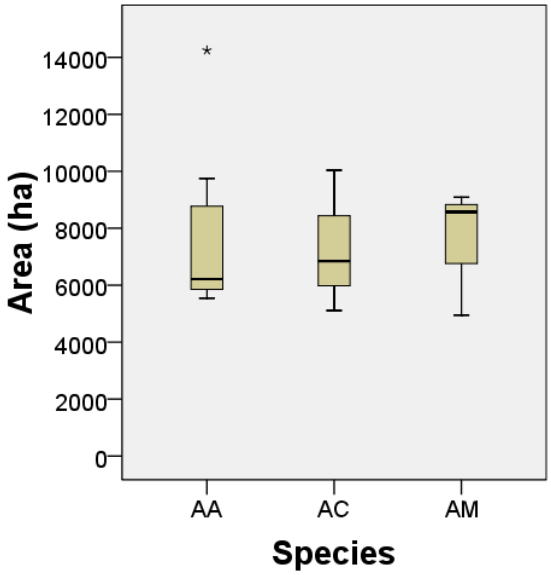

Fig. 11. The size of breeding season ranges (ha) among macaws species, generated by the KDE, were not significantly different from each other ($p = 0.350$).

There was no difference in range size (p = 0.133) among species during the non-breeding season (Fig. 12).

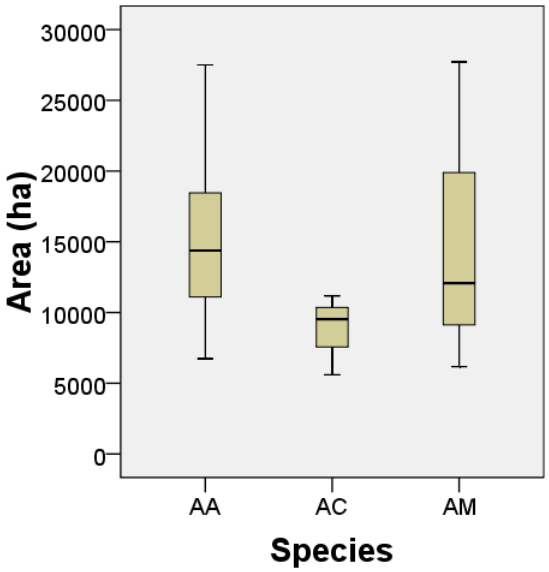

Fig. 12. The size of non-breeding season ranges (ha) among macaws species, generated from the KDE, were not significantly different from each other (p = 0.133).

Seasonal differences in range size

Mean range size (estimated using KDE) between breeding season and non-breeding season (Fig. 13) was significantly different for *A. ararauna* (p = 0.012). Mean range size for *A. chloropterus* and *A. macao* did not vary significantly in size between seasons (p = 0.593 and 0.285 respectively).

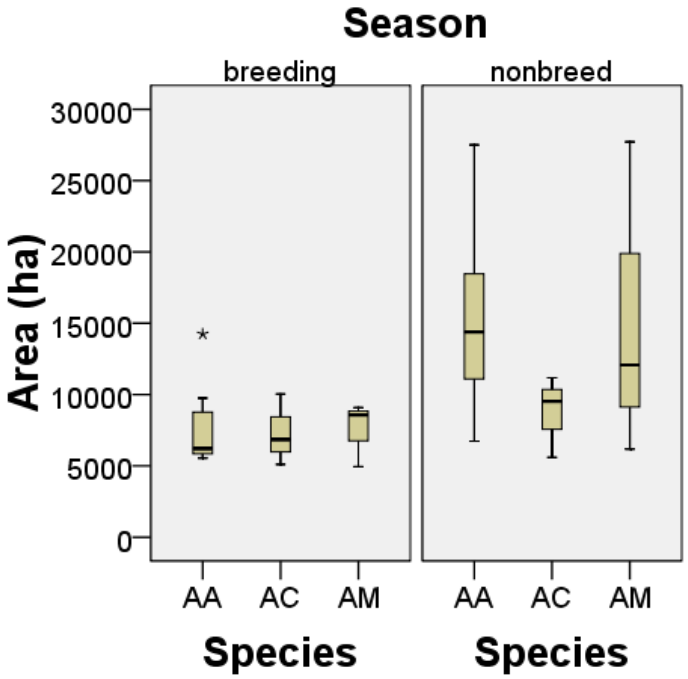

Fig. 13. Range size was significantly larger for *A. ararauna* during the non-breeding season (p = 0.012), but range sizes for *A. chloropterus* and *A. macao* were not significantly different between seasons (p = 0.593, 0.285 respectively). (Based on KDE).

Home range size estimated using the MCP estimator (Fig. 14), was significantly different for *A. ararauna* between seasons (p = 0.012). Mean ranges for *A. chloropterus* and *A. macao* did not vary significantly in size between seasons (p = 0.109 and 0.285 respectively).

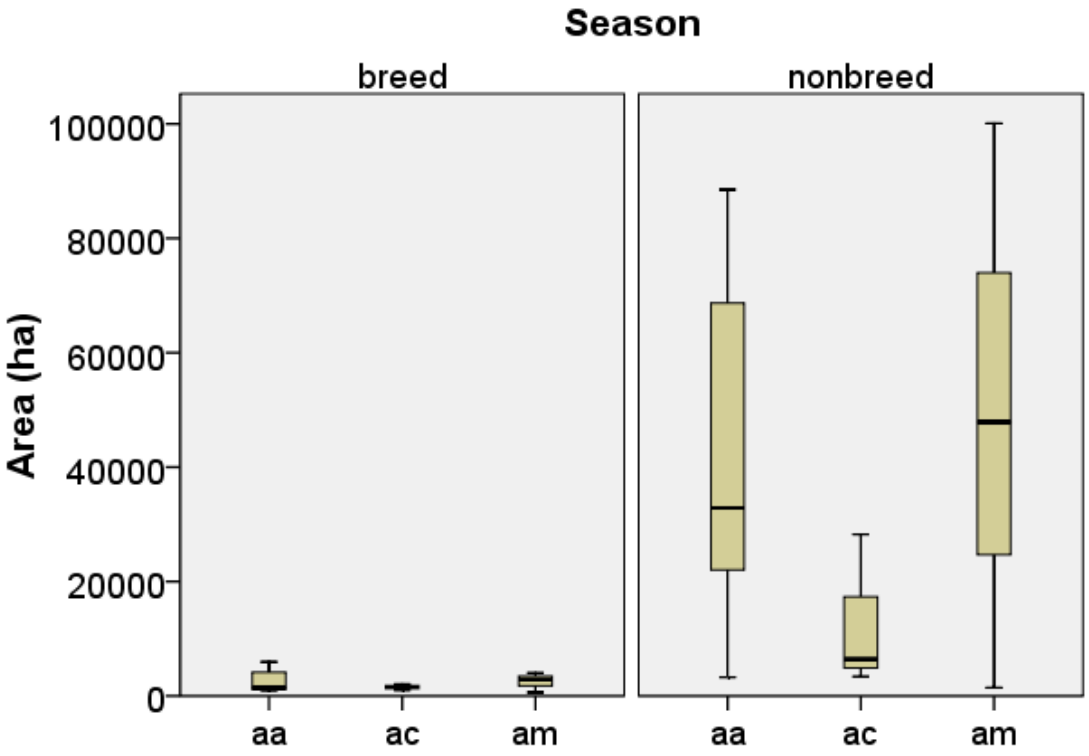

Fig. 14. Differences in range size (ha) between breeding season (left) and non-breeding season (right) were only significant for *A. ararauna* (p = 0.012). Significance values for *A. chloropterus* and *A. macao* were p = 0.109 and p = 0.285 respectively. Two outliers of *A. ararauna* during the non-breeding season excluded from this figure had values of 461,913 ha and 538,609 ha. (Based on MCP).

Home range overlap

Overlap between breeding individuals of each species was only calculated for breeding season (Table 13). As expected, the values of overlap differed from each other, but it is clear that *A. ararauna* ranges have a higher degree of overlap than *A. chloropterus* and *A. macao*. This agrees with the sociable nature of macaws. The overlap values for *A. chloropterus* were higher than expected, due to the sharing of space at the

clay lick that is outside of the usual geographic range of activities. From field observations of other nesting individuals which were not included in the home range analyses, *A. chloropterus* had the least amount of overlap among individuals than the other species.

Table 13
Amount of overlap between individual ranges for each species during the breeding season using BA and UDOI indices for the 3-D density surfaces generated by the KDE, and percent overlap for the 2-D surfaces generated by the MCP estimator. *Ara ararauna* had the highest degree of overlap among individuals for all indices measured.

Overlap Measure	*Range of values*	*AA*	*AM*	*AC*
UDOI	> 0	4.44 ± 0.28 SE	1.86 ± 0.48 SE	1.92 ± 0.94 SE
BA	0-1.0	0.86 ± 0.02 SE	0.58 ± 0.06 SE	0.58 ± 0.09 SE
% overlap MCP	0-1.0	0.54 ± 0.05 SE	0.38 ± 0.31 SE	0.30 ± 0.04 SE

Distance measures

During the breeding season, the MDC among the different species of macaws did not differ significantly (Kruskal Wallis; p = 0.13) (Table 14), nor did it differ significantly for the non-breeding season (p = 0.089) among species of macaws. The only macaw species that differed in MDC between seasons was *A. ararauna* (p = 0.036). The MDC for *A. macao*, and *A. chloropterus* did not change between seasons (p = 0.109 and 0.593 respectively). The mean MDC of unknown/non-breeding individuals of *A. chloropterus* (ACnb) also did not differ significantly from other species, nor between seasons (p = 0.144), however, the center of activity (clay lick) for these individuals did not remain constant as they moved in and out of the monitoring area, and no inferences should be made. Maximum distances located were greatest for *A. ararauna* (Fig. 15).

Table 14
Mean distances (m) of macaw locations from a centre of activity (nest or clay lick) for breeding season and non-breeding season. Within each season, there were no interspecific differences in MDC, and seasonal differences were only exhibited for *A. ararauna*, when mean distances from the centre of their range were significantly greater* during the non-breeding season (br = breeding, nb = not-breeding).

		Breeding season				*Non-breeding Season*			
Species	N	Mean Max. Dist.	Mean MDC	SE	N	Mean Max. Dist.	Mean MDC	SE	Difference in MDC by season
A. ararauna	8	6520	2171	256	8	59973	6022	1188	p = 0.036*
A. macao	3	5212	1414	400	3	40988	2892	1083	p = 0.109
A. chloropterus (br)	3	5418	1948	812	3	18253	2134	576	p = 0.593
A. chloropterus (nb)	4	13906	5702	1676	4	26150	9730	2838	p = 0.144
Difference in MDC by species			p = 0.130				p = 0.089		

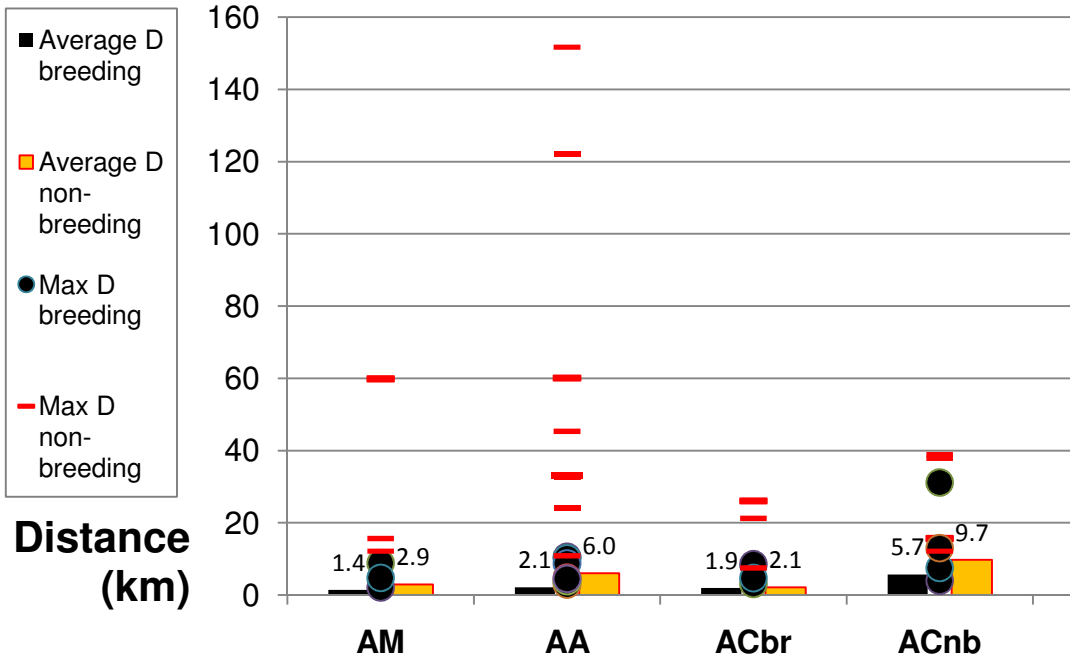

Fig. 15. The mean distance of macaw locations from the center of activity (MDC) is slightly greater during non-breeding season, but only significantly greater for *A. ararauna* ($p = 0.036$). Maximum distances flown by individuals of each species are shown for reference (red lines).

Habitat selection

Habitat selection (Neu et al. 1974) was analyzed for *A. ararauna* during the dry season (Table 15). They significantly preferred floodplain vegetation, lowland terrace, and palm swamps. All types of highland forest and bamboo forest were significantly avoided.

Similar results for vegetation type were obtained from the area-based sampling using buffered resource units of 2500 m (19.6 km^2), except that at this larger scale a stronger degree of habitat preference and avoidance was exhibited (Table 15). At this

scale, which is based on habitat composition, mixed palm forest and mid-terrace forest were additionally preferred, and secondary forest and anthropogenic areas were avoided. Although palm savannah existed in the study area, marked macaws were not observed using this habitat during the study period (Fig. 16).

Table 15
Habitat selection results for *A. ararauna* during the dry season comparing used resource units and available resource units at the sample point (n = 803 for each resource unit type). For vegetation type, area-based sampling generated stronger selection for (+) or against (-) the vegetation types that had a non-significant outcome (ns) in the point-based analysis.

Attribute	*Type*	*Outcome*	*Outcome*
Vegetation	Floodplain	+	+
	lowland terrace	+	+
	palm swamp	+	+
	bamboo	-	-
	bamboo mixed	-	-
	flooded forest	-	-
	highland terrace forest Alluvial	-	-
	highland terrace forest Colluvial	-	-
	highland hilly forest	-	-
	Anthropogenic	ns	-
	Mid-terrace Forest Alluvial	ns	+
	Palm swamp mixed	ns	+
	Secondary Forest	ns	-
Ecozone	Humid subtropical	+	n/a
	Very Humid Subtropical	+	n/a
	Humid Tropical (Transition) to Very Humid Subtropical	-	n/a
	Humid subtropical (Transition) to Humid Tropical	ns	n/a
	Humid Tropical	ns	n/a
	Very Humid Premontane Tropical (Transition to humid Tropical)	ns	n/a
	Pluvial Subtropical	ns	n/a
	Pluvial Semisaturated Subtropical	ns	n/a
Geology	Ipururo formation	+	n/a
	Madre de Dios Formation	+	n/a
	Recent Alluvial Deposit	-	n/a
	Subrecent Alluvial Deposit	-	n/a
	Foothill Alluvial deposit	ns	n/a
	Huayabamba group	ns	n/a

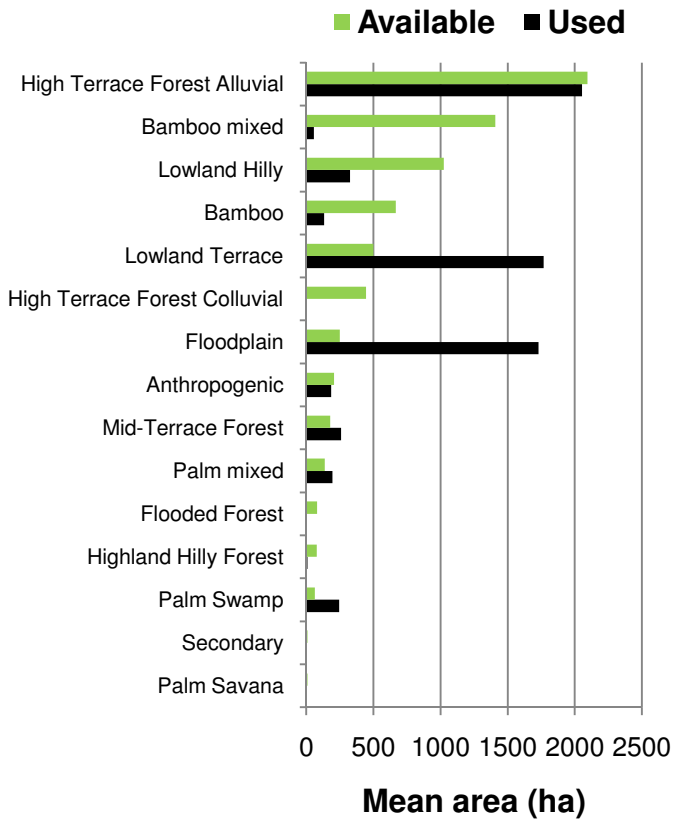

Fig. 16. Mean area (ha) of each habitat type available to *A. ararauna*, and used by *A. ararauna* (n = 803 of each resource unit type), which showed a higher proportional use of lowland habitats (floodplain, lowland terrace and palm swamps), which was confirmed as preferred in the habitat selection analysis.

Other area-based habitat attributes tested (Table 16) showed that lowland habitat was a significant component of the used plots, with a mean elevation of 255 m (range from 0 to 334 m) whereas mean elevation of the available plots was 307 m (range from 0 to 563 m). The mean proximity to communities and roads was significantly less in the used plots (33,786 m + 355 SE and 24,933 m + 274 SE) than available plots (79,482 m + 1,848 SE and 52,386 m + 1,372 SE), which was expected due to several of the seasonal

locations occurring in close proximity to the road and its communities. Finally, water courses (measured as the length of major rivers and minor streams within each plot) occurred significantly more in used plots than available plots (mean length of 4,998 m + 158 SE and 1,439 m + 88 SE). There were significantly more habitat types in the used plots (7) than the available plots (4).

Table 16
All mean values of habitat attributes were significantly different between used and available sample units within the study of *A. ararauna* during the dry season.

Plot	*Attribute*	*Used (n=803)*	*Available (n=803)*	*Significance**
point	elevation (m)	255	307	<0.00001
distance	to community (m)	33,786	79,482	<0.00001
	to road (m)	24,933	52,386	<0.00001
area (1km diam)	water (m/plot)	4998	1439	<0.00001
area (5km diam)	habitat richness	7.3	3.9	<0.00001

*Wilcoxon Signed Ranks paired-sample t-test

Proximity to palm habitat

The mean distance of macaw locations to a wetland (palm swamp, mixed palm forest, or palm savannah) was 1,751 m + 94 SE, whereas the mean distance from random points to a wetland was 21,575 m 715 SE (Fig. 17). When macaw locations were compared to random locations throughout the landscape, they were significantly closer to wetlands than expected by chance ($p < 0.001$).

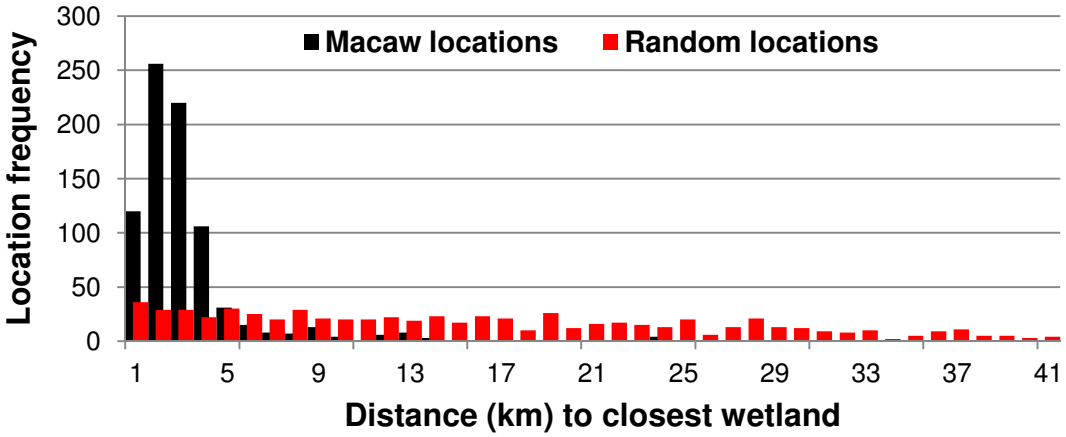

Fig. 17. Macaw locations were closely associated with wetlands, and significantly closer to wetlands than randomly sampled locations were ($p < 0.001$).

When examined by wetland type, it was evident that there was a closer association with palm swamps (pure palms) than with palm mixed forest. Mean proximity to palm swamps was 2,191 m + 127 SE, and proximity to palm mixed forest was 6,576 m + 116 SE (Fig. 18).

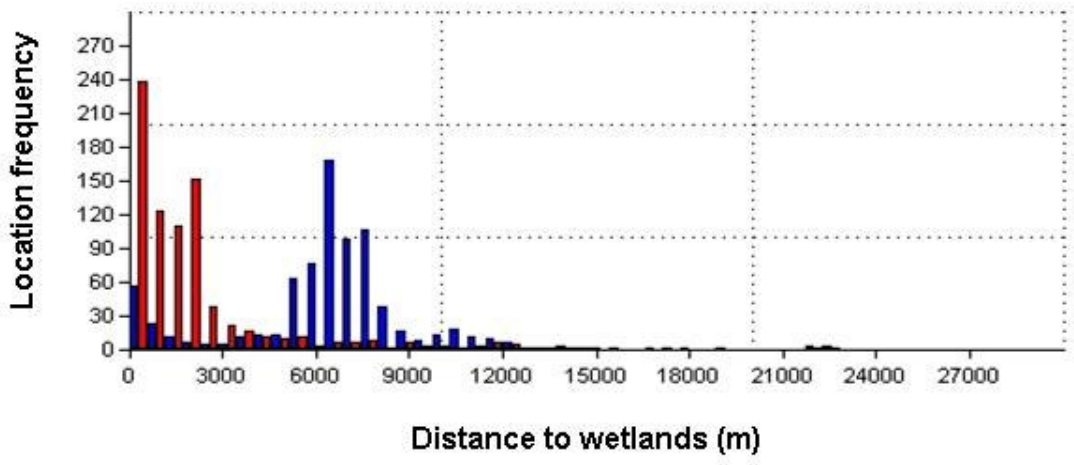

Fig. 18. Macaw locations were significantly more associated with pure palm stands (red) than mixed palm forest (blue), yet both wetland types are highly correlated with proximity to macaw location.

Patch analysis

The distribution of wetlands was concentrated in the southern region of the study area, which was associated with movements throughout this area during the dry season. To explore whether there were additional differences in this region than the other regions which were "not used" even after several seasons and extensive searches, patch metrics were quantified to describe each landscape (Table 17).

Table 17
Patch metrics for used (U) landscape and not-used landscape (N).

Habitat Types	Mean Patch Size		Patch Density		Median Patch Size		Patch Size Standard Deviation	
Preferred habitats	N	U	N	U	N	U	N	U
Floodplain	53.29	319.9	0.019	0.003	2.00	2.0	440.41	3493.2
Lowland Terrace	519.46	185.6	0.001	0.012	3.00	2.0	2313.44	1146.3
Palm swamp	143.28	263.1	0.007	0.004	4.72	18.7	419.99	□77.5
Mid-Terrace	379.61	439.2	0.003	0.002	2.40	1.4	1482.29	2105.1
Palm mixed	1329.38	363.6	0.001	0.003	356.65	13.6	2058.78	1200.1
Mean	**485.01**	**314.28**	**0.006**	**0.005**	**73.75**	**7.53**	**1342.98**	**1724.42**
Avoided habitats	N	U	N	U	N	U	N	U
Bamboo forest	1963.22	331.1	0.001	0.003	2.66	13.1	16395.60	1532.8
Bamboo mixed	4744.83	462.1	0.000	0.002	7.37	3.3	31088.70	2187.5
High Terrace Alluvial Forest	2191.02	1961.4	0.000	0.001	1.44	1.3	16602.72	18197.9
High Terrace Colluvial	641.70	0.0	0.002	0.000	2.00	0.0	6601.32	0.0
High hilly forest	777.02	3.2	0.001	0.333	1.18	3.2	2676.77	0.0
Low hilly forest	1966.63	2019.2	0.001	0.000	4.00	21.7	8311.32	4084.2
Secondary Forest	1.44	3.3	0.697	0.301	0.68	1.0	2.08	8.1
Flooded Forest	127.17	30.6	0.008	0.033	2.40	1.7	646.60	163.5
Mean	**1551.63**	**601.36**	**0.089**	**0.084**	**2.72**	**5.67**	**10290.64**	**3271.76**

In general, there was not a great difference in habitat diversity or evenness between the “used” region and the “not-used” region (SDI = 1.70 and 1.98, SEI = 0.63 and 0.73 respectively). In the “used” region, diversity and evenness were lower, which may suggest that habitat diversity and heterogeneity have less to do with landscape use than the type of habitats present. The mean size of “preferred habitats” (as determined in habitat selection) was smaller, the median patch size was also smaller, and the patch size standard deviation was greater in the used region, suggesting that patches of “preferred habitats” were highly variable in size, and created a mosaic of accessible choices across the landscape. Indeed, there were large contiguous stretches of “avoided” habitat in the northern/western portion of the study area where marked macaws had never been recorded. These habitats also occurred in the “used” area, but mean patch size was much smaller. Overall, mean patch size of both “preferred” and “avoided habitat” was smaller in the “used” area than the “not-used” area, suggesting that mean patch size may not be an important factor in landscape selection.

DISCUSSION

Inaccessibility and behavioral characteristics of macaws have historically hindered research on their movements (Casagrande and Beissinger 1997; Gilardi and Munn 1998; Renton 2002). This is the first study to describe seasonal movement patterns by macaws in the Amazon, and to quantify space use by the breeding populations of *A. ararauna*, *A. chloropterus*, and *A. macao*.

All species of macaws had similar home range sizes during the breeding season, ranging from a mean of 1,540 ha ± 312 SE (*A. chloropterus*), 2,508 ha ± 993 SE (*A. macao*) and 2,541 ha ± 690 SE (*A. ararauna*) using the MCP estimator. Seasonal variation existed for all macaw species. Non-breeding ranges were larger at 12,674 ha ± 7,828 SE (*A. chloropterus*), 49,815 ha ± 28,487 SE (*A. macao*), and significantly larger for *A. ararauna* (117,849 ha ± 57,654 SE). The KDE overestimated the home range size during breeding season, and either underestimated, or failed, for non-breeding and total ranges.

During the breeding season, site fidelity was maintained by all individuals that had established nesting sites. Overlap among home ranges was greatest for *A. ararauna* which is not surprising considering their social nature, large flock sizes, communal roosting (Gilardi and Munn 1998; González 2003; Brightsmith 2005), nesting, and foraging regardless of nesting status. In contrast, home ranges of breeding *A. chloropterus* were discrete; tagged breeding pairs foraged alone and this behavior was observed by other non-tagged pairs as well. Home ranges for breeding *A. chloropterus*

were actually more discrete than reported here. The clay lick, where all individuals visited erratically over the breeding season, was included in the overlap analysis. This area is a site of complete overlap, but is outside of their typical range of movement, thus the amount of home range overlap was overestimated.

During the non-nesting season, which also corresponds with the dry season, site fidelity was maintained for individuals of *A. macao* and *A. chloropterus* that nested, but not for *A. ararauna*. Although this is based on home ranges of only three individuals of *A. macao* and *A. chloropterus*, these individuals nested in the same sites each year and used the same area. Transmitter or nest failure of other nesting individuals prevented calculation of their home ranges, but in terms of site fidelity, these individuals used the same nests each season and for the duration they were nesting, and even during non-nesting season, had similar movement patterns and space use of marked nesting individuals.

The mobility of *A. ararauna* is exceptional, which is demonstrated by some individuals being located farther than 160 km from the breeding site. Migrations to the Bolivian side of the border were not possible to monitor. Consequently, the extent of landscape used before their return to the breeding range may be considerably greater. One individual was located by aircraft at a clay lick 90 km away (Colpa Colorada, on the Tambopata river) and its proximity to the clay lick (although not visually confirmed) was recorded for a week by a data-logger installed near the lick. The pattern of movement during each season was towards the south and southeast of their breeding

range. The landscape north and west of the breeding area was not used, even though this region was covered extensively during the overflights.

While the method of using MCP to generate home ranges is known to overestimate when outliers exist in a dataset, dry season ranges for *A. ararauna* are in fact underestimated, but given that 11 individuals used a minimum of 1,280,467 ha (12,805 km^2) over four months of the dry season, it is clear that *A. ararauna* use extensive areas of the landscape to satisfy their resource requirements.

The movements of *A. chloropterus* tagged at the clay lick were extremely wide-ranging; they eventually left the area and it was not possible to relocate them during overflights. Only two of 15 of these individuals remained in the region and nested the following year. Unfortunately, the transmitter failed before recapture was possible for one pair, and the nest of the other pair failed, and they subsequently left the area. Of three pairs opportunistically tagged individuals competing for two cavities, none nested in any, and the last location of one of these marked pairs was close to the foothills of the Andes. This suggests that movements of individuals with established nests and those without established nests (young/old, unmated, cavity limitations) may be substantially different for *A. chloropterus*, and potentially for *A. macao* as well.

In the western Amazon, seasonal, yet contrasting patterns of fluctuations of macaw abundance have led to speculation that macaws make large-scale seasonal movements (Karubian et al. 2005) and alter their use of habitats (Renton 2002) which may possibly be related to resource tracking (Renton 2001, 2002). The results of this study demonstrate that macaws do fly long distances, and seasonal variations in

movements do exist, yet the patterns of these movements are not equal for all species or sectors of the population. *Ara ararauna*, which is ecologically similar and co-exists with *A. chloropterus* and *A. macao* behaves much differently, which was also noted by Renton (2002) and Karubian et al. (2005). There also appears to be two behaviorally distinct sectors within a population of *A. chloropterus* and *A. macao* which may relate to differences seen in movement patterns.

All macaw species in the study exhibited long-distance movements; however these movements varied in duration, frequency, and fidelity. Long-distance movements may be more related to established nest sites rather than to resource tracking. Nesting cavities have been shown to be a limited resource, especially for secondary nesters such as macaws (Gibbs et al. 1993; Mawson and Long 1994; Newton 1994; Poulsen 2002; Cockle et al. 2010)(KA pers.obs) not all macaws of breeding age may be able to nest. Although numerical estimates are lacking in the literature, it is believed that only a small proportion of macaws actually nests each year, leaving a large number of mobile individuals free from activities associated with nesting (searching, establishing, nesting, defending, etc.).

Seasonal fluctuations in abundance: a combination of habitat requirements, behavior, climatic factors and survey methodology?

The objective of this study was not to monitor changes in relative abundance; however, several insights may provide explanations for the apparent seasonal variation in abundance of macaws observed by other researchers in the Neotropics. Renton (2002)

reported that *A. chloropterus* and *A. macao* abundances declined three-fold in the dry season, yet in Ecuador, macaw abundance declined (but not significantly) (Karubian et al. 2005) as well as general parrot abundance (Newton 1994; Sosa-Asanza 2000) in the wet season. In the eastern part of Ecuador, macaws (*Ara ambiguus guayaquilensis*) were completely absent in November and March (Berg et al. 2007) which are the transition months between seasons, and in northern Costa Rica the abundance of *A. ambiguus* declined in the wet season. In central Mexico, *Ara militaris* were less abundant in the dry season (Contreras-González et al. 2009). Karubian et al. (2005) felt their results were contradictory to the expected patterns of seasonal fluctuation, but caution must be used when applying the broad generalization that macaw abundances decrease during the dry season (Renton 2002) to other sites and other species.

Instead of discussing abundance in terms of declines or macaws *leaving* an area, it may be more informative to approach this puzzle by thinking in terms of macaws *arriving* to an area. Many of the study sites are within floodplain habitat which is believed to have a higher density of nesting substrates. The breeding season, regardless of month or amount of precipitation, has the highest relative abundance of macaws in the Peruvian rainforest (Renton 2002; Brightsmith and Munoz-Najar 2004), in the Ecuadorian Amazon (Sosa-Asanza 2000; Karubian et al. 2005), in the tropical dry forests of central Mexico (Contreras-González et al. 2009) and the Atlantic lowland forests of northern Costa Rica (Powell et al. 1999). Other studies in Ecuador (Berg et al. 2007), Costa Rica (Vaughan et al. 2006b; Matuzak et al. 2009) and Belize (Renton 2006) were focused on diet; not on seasonal changes in macaw abundance, so it is not known if

the same pattern would be revealed. This strongly suggests that it is the reproductive season, not fruit availability or precipitation that is correlated with macaw abundance.

Seasonal differences in macaw detectability may result in over or under estimation of actual densities, and may be factor in apparent population fluctuations. The breeding season is a period when macaws are more vocal, more active, and more detectable. Macaws are difficult to count accurately; a nesting pair may visit the nest hourly, foraging individuals may move locations every 20 minutes, the same group may be mistaken for different groups throughout the period of observation, and groups may be counted that are just passing over and don't actually remain in the area. During the dry season, marked individuals (with the exception of *A. ararauna*) remained in the breeding area, and despite the lack of vocalization, their presence was confirmed because of their transmitter signals. Macaws can also be deceptively quiet, especially when they are foraging (Munn 1988), which can often be up to several hours in the same tree.

Seasonal resource tracking

Other studies have reported seasonal fluctuations in macaw abundance, yet the cause of this was unknown. One explanation was that macaws were responding to seasonal scarcity in food resources, and tracking these resources as they became available across the landscape. Problems associated with estimating macaw abundance, defining the macaw population, behavioral differences within that population itself, and whether scarcity actually exists when availability data and inconsistent findings brings

this broad generalization to question. Macaws, which differ in their food preferences, resource needs, movements, and breeding requirements, cannot be expected to respond equally to the same environment, and especially to environments that are vastly different.

Seasonal resource tracking in the context of migrations related to the timing of fruit availability was not studied, but *A. ararauna* appear to do spatial tracking of an important resource. This species does not seem to follow the trends observed by other researchers that have observed the three species simultaneously (Renton 2002; Burger and Gochfeld 2003; Karubian et al. 2005). In this study, of the three macaw species studied, only *A. ararauna* undertook seasonal migration. This is particularly interesting given that this was the only species in Renton's and Karubian's study that did not exhibit seasonal fluctuations in abundance. Results of space use suggest that the landscape is not used randomly by *A. ararauna*. Given their long life span, and the experience accumulated in that time, it stands to reason that macaws are intimately familiar with extensive areas of the landscape. Even marked individuals from geographically distinct breeding areas were located together during the dry season. Similar predictable, seasonal, and directional movement patterns were seen by *Amazona farinosa* in Mexico (Bjork 2004). She noted that while the area covered by *Amazona farinosa* was significant (10,000 km^2) it was the consistency and use of specific locations that was more significant. These seasonal movements of *A. ararauna* may be related to tracking of palm swamps which will be discussed in the next section.

Key habitats and landscapes

Several important habitats for macaws were revealed by this research. Habitat preference was not determined for *A. chloropterus* and *A. macao*, or *A. ararauna* during the breeding season, because the data provided by the habitat map was not fine-scale enough for the small ranges. Although the movements of *A. chloropterus* tagged at the clay lick matched the scale of the habitat map, the number of locations obtained was insufficient to be a representative sample for habitat analysis. Despite not quantifying habitat preference under these circumstances, general preferences for all species can still be speculated based on observations made by this and other studies.

Floodplain habitats and lowland terrace adjacent to major waterways were important habitat in this study, and were commonly associated with macaws in other studies. However, this association of macaws with floodplain habitat is also associated with choice of study site; this study and other studies of macaws in the Amazon were logistically based adjacent to major rivers (Munn 1988; Renton 2002; Karubian et al. 2005; Brightsmith 2005). Although sampling bias cannot be ignored, several observations indicate that these speculations of floodplain forest/lowland terrace habitats as important habitats may have some merit.

During searches for new foraging species and nesting sites, the presence of macaws did seem markedly less in tracts of forest further from the river which did not contain landscape features associated with riverine habitats (lakes, swamps, flooded forest, and successional patches). On various excursions to explore other regions (Tambopata), the forest on the higher terraces, 1 to 2 km from inland from a major river,

was almost devoid of macaws. One would walk all day and not detect a single macaw, whereas closer to the river, macaw activity was markedly different. Macaw presence decreasing with distance was also noted by researchers studying density in relation to distance from the Colorada clay lick on the Tambopata River (A. Lee pers. comm.).

Given the inherent problems associated with sampling methodology and macaw detectability, I do not mean to imply that contiguous stretches of forest are unimportant habitat for macaws. Even though floodplain and lowland terrace may provide a higher density of nesting substrates, their relative area in the landscape is small and cannot possibly support the bulk of macaw populations. Marked individuals of *A. chloropterus* did use the forested regions further inland, and while in the area, maintained larger ranges than their marked breeding counterparts that had territories closer to the river. Tracking these macaws by ultralight aircraft provided an informative view of the extensive landscape; most striking was the uniform distribution of emergent trees towering high above the dense canopy (believed to be *Dipterix micrantha*, but aerial photography during the flowering cycle would be necessary to confirm this).

Broader implications

The mobility of macaws allows them to acquire the resources they need over a vast area. Renton (2002) speculated that a variety of habitats and forest types may be required to sustain healthy populations of macaws; her comments were mirrored by Karubian (2005). With the exception of *A. ararauna* during the dry season, breeding macaws lack this mobility which would make them more sensitive to reduction in habitat

quality, configuration or size. Considering that breeding individuals are the only ones that affect population size, conservation efforts should be concentrated on determining their annual resource requirements and critical habitats for sustaining a viable population.

Finally, despite the small sample sizes, the breeding home range sizes estimated here have a moderate probability of being representative for resident breeders of this area. After following the same individuals for several years, space use did not vary much from year to year, and although home ranges were not calculated for all breeding individuals, the locations collected and signals detected indicated the size of are they occupied was similar. Furthermore, for *A. chloropterus*, two individuals captured at the clay lick that found nests had small ranges until their nests failed and they left the area, presumably searching for other potential nesting habitat. Other nesting *A. chloropterus* did not always nest each year, but maintained the same small nesting territory. Little is known for non-breeding *A. macao*, so these results should not be applied to general macaw populations. Furthermore, inferences to other sites should be made cautiously, because the landscape is highly variable and how other populations respond to their environment may be different as well.

CHAPTER II

INTRODUCTION TO RESOURCE USE

The three species of macaws studied in this research (*Ara ararauna*, *A. chloropterus* and *A. macao*) co-exist spatially and temporally. They are morphologically similar, breed in the same area over the same period of time, require tree cavities for nesting, and are frugivores which that specialize on hard immature seeds. It is reasonable to expect that some degree of resource partitioning, which is defined as the "differential use by organisms of resources such as food and space" (Schoener 1974) may occur among these ecologically similar species.

Previous studies speculate that seasonal fluctuations of macaw abundance may be related to food scarcity, however the cause and scale of these seasonal fluctuations remains unclear (Karubian et al. 2005). Many bird species have adopted a flexible foraging strategy to utilize different items as they become seasonally available (Rowley and Chapman 1991; Galetti and Rodrigues 1992; Wermundsen 1997). Seed predators that forage in the canopy were found to be particularly responsive to seasonal variation of canopy trees across the landscape (Renton 2001), so it is important to describe food resource use by macaws in a temporal context of when these resources are available, and when macaws actually use them.

Macaws, like many parrots, are seed predators (Howe 1980; Galetti and Rodrigues 1992; Trivedi et al. 2004) that specialize on immature seeds (Munn 1988), and are able to consume fruits with hard pericarps (Gilardi et al. 1999). Many immature

fruits have chemical defenses such as tannins, phenols, and other plant chemicals (Wrangham and Waterman 1983; Balandrin et al. 1985) that can be toxic to many animals (Kinzey and Norconk 1993; Gilardi et al. 1999). Macaws, through the consumption of clay (geophagy) may have the ability to detoxify substances (Munn 1988; Gilardi et al. 1999), possibly giving macaws a competitive advantage over other frugivores that are unable to consume these immature fruits (Munn 1988).

Due to the chemical and mechanical constraints posed by immature fruits and their location in the forest canopy, as well as the greater abundance of immature fruits relative to mature fruits, food resources may be superabundant and actual competition among macaws may be either low or non-existent (Gordon and Illius 1989) despite their ecological similarity. Comparing dietary breadth and overlap can indicate the degree of dietary specialization and the nature of competitive interaction among species of macaws.

Previous work showed that dietary overlap among closely related species can be greater during periods of high fruit availability (typically wet season), and lower during times of food scarcity (typically dry season) (Janson and Emmons 1990; Peres 1994; Wahungu 1998; Stevenson et al. 2000). During periods of food scarcity, animals may turn to unique and alternative food sources (Galetti 1993; Kinzey and Norconk 1993; Ragusa-Netto 2004, 2005); thereby minimizing competition between closely related species if these resources differ among species. One would expect the degree of overlap among macaw species to be less during the dry season, and diet breadth to be greater as

they turn to alternate, but not shared food resources. Diversity and niche measurements can thus lend insight to interspecific and seasonal differences in macaw diets.

Antagonistic interactions were rarely observed during foraging events, yet aggressive displays were observed in proximity to nesting cavities, indicating resource limitation induced competition for nest sites. Nesting resources are rarely abundant for secondary cavity nesters (Forshaw 1989; Gibbs et al. 1993; Renton 2004; Brightsmith 2005) such as macaws. Both intraspecific and interspecific competition over nesting resources has also been reported by other researchers in the region (Renton 2004; Brightsmith 2005) The importance of obtaining data on nesting resources is emphasized by the fact that only 1 or 2 offspring (Forshaw 1989) are produced each season per breeding pair, and by some estimates, only 5% successfully reproduce (Munn 1988).

Although home ranges provide critical information on space use, it is just as important to understand what resources macaws are utilizing, and when they are using them. Identification of resources, their availability, and quantification of their relative importance has been the driving force behind understanding the interaction between an animal and its habitat and is an essential first step towards conservation of their habitat.

This work has meaningful implications for conservation in this region, because the rate of settlement predicted by expansion of the road network into forested regions (Killeen 2007), and the trend towards larger-scale land use activities and mechanized agriculture (Shoobridge 2006) will result in an irreversible alteration of the landscape in the southwestern Amazon. Availability of food resources (Saunders 1986; Martin 1987; Gnam and Rockwell 1991; Saunders et al. 1991; Powlesland et al. 1992; Thiollay 1993)

and nest site availability (Saunders et al. 1982; Snyder et al. 1987; Newton 1994; Inigo-Elias 1996; Holt and Martin 1997; Arias et al. 2000; González 2003; Renton 2004) can limit bird populations. The removal of nesting and foraging resources to birds and other wildlife during land-clearing or forestry practices is thus far small-scale, so we have a unique opportunity to establish baseline data of resource use by macaws while the landscape is relatively intact.

My objectives are to identify food and nesting resources used by macaws throughout the year, and describe seasonal variation in resource use and selection.

METHODS

Study area

The study area encompasses a circular area of 160km radius from the confluence of the Madre de Dios River and Los Amigos River in the department of Madre de Dios (Fig. 19). This extent was determined by the furthest recorded movements of marked macaws from the principal site where nesting and research activities occurred (Centro de Investigación y Capacitación Rio Los Amigos) (UTM: 380500E 8610297N). The majority (82%) of Madre de Dios is lowland tropical forest less than 500 meters above sea level (masl) and the Los Amigos Conservation Concession ranges from 222-437 masl (Pitman 2008). Dissecting this landscape are meandering and braided rivers of varying sediment loads, streams, oxbow lakes and swamps. Major rivers in the area are the Madre de Dios, Colorado, Iñambari, Tambopata, Piedras, and Manú.

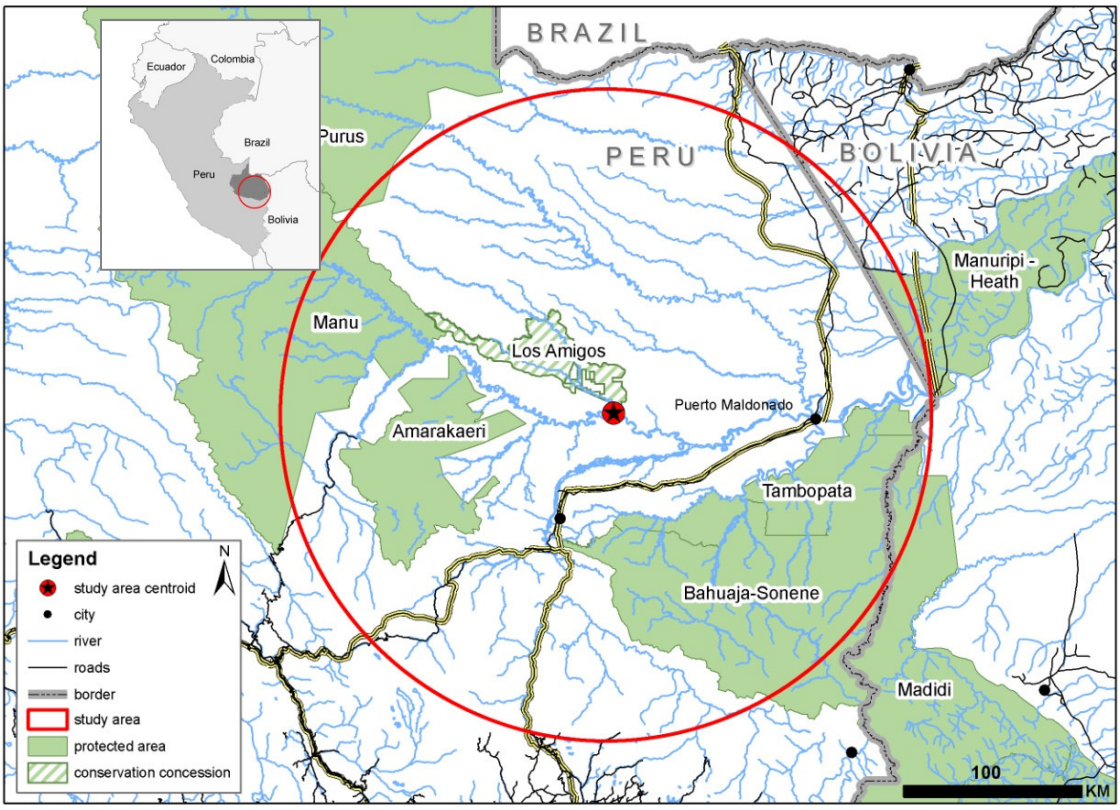

Fig. 19. The study area in southeastern Peru is within the department of Madre de Dios (inset) and part of the Amazon basin. Research activities were based out of CICRA (Centro de Investigación y Capacitación Rio Los Amigos) and extended throughout the study area (red circle) according to the movements of tagged macaws.

The Madre de Dios watershed is one of the wettest regions of the Amazon basin where annual precipitation can exceed 4,000 mm (McClain and Naiman 2008). In general, precipitation increases from east to west (Hamilton et al. 2007), and seasonality becomes more marked from north to south (Gentry and Ortiz 1993). Mean annual rainfall recorded by the weather station at CICRA between 2000-2006 was between 2,700 and 3,000 mm, with a maximum of 3,498 mm in 2003, and a minimum of 2,152 mm in 2005 (Pitman 2008). The wet season (October-May) receives over 80% of the

annual rainfall, where January is the rainiest month (Pitman 2008), and dry season extends from May-September, with August being the driest month.

The dry season is also characterized by events called “friajes”, first reported in 1992 (Morize 1922) and again in 1942 (Serra and Ratisbona 1942) which are caused by the movement of polar air masses from the south, resulting in change of climatic conditions in Amazonia and southeastern Brazil (Marengo et al. 1997). These events, which can produce frost in some areas, last between 3-5 days, and occur frequently (Culf et al. 1996). Cold fronts (“friajes”) occurred from May through September with temperatures generally below 15°C and as low as 10°C. The number of events from 2004-2008 ranged from 5-10 per dry season and lasted from 3-7 days. Between 2005 and 2007, Pitman (2008) described 14-17 “friajes” (daily minima < 20°C) and 4-5 severe “friajes” (<15°C) per winter.

This region is dominated by broadleaf evergreen or semi-evergreen tropical forest (Osher and Buol 1998). The landscape of southwestern Amazon is generally classified into two broad categories: upland forest (terra firme) and lowland forest (flooded, seasonally flooded). Two kinds of uplands were categorized based on physiography: terraced uplands which are flat and lightly dissected by small streams, and hilly uplands which are highly dissected and extend north and northwest for hundreds of kilometers (Foster 2001). Within these categories, other vegetation consists of bamboo thickets (Hamilton et al. 2007), palm swamps (Kalliola et al. 1991), tropical savannah, and extensive floodplains of varying successional stages (Kvist and Nebel 2001). This

region is also characterized by clay licks (Emmonds and Stark 1979) which are commonly associated with river-edges, although they can also occur in forested regions.

Considering the Amazon has greater than 30,000 species of plants (Gentry 1982), and is a mosaic of varying precipitation patterns, soil types, topography, hydrology, and geological history, great effort is being devoted to distinguishing vegetation types. Satellite imagery and remote sensing has revealed that there may be hundreds of unique forest cover types in the Peruvian Amazon alone (Tuomisto et al. 1995).

This is a relatively undisturbed and sparsely populated region, yet colonization of mid and lower elevations is increasing (Mena et al. 2006), spurring concern for this highly biodiverse area (Tuomisto et al. 1995; Tuomisto 1998; Patterson et al. 1998; Macquarrie 2001; Goulding et al. 2003). Currently, land use in the area is a mixture of small private land-holdings, small-scale agricultural fields, pastures, small communities, mining concessions and forest concessions; most of which are concentrated along major waterways and the Interoceanic highway, of which this last frontier section is currently being paved. A network of protected areas and indigenous reserves is bisected by the Interoceanic highway which connects Brazil with the Peruvian coast.

Data collection and processing

Dietary items

Feeding data were collected on radio-tagged and non-tagged macaws throughout the year from January 2004 to January 2008. Foraging observations were made by experienced observers looking and listening for falling fruit or other signs of macaw

presence along established trails and by canoe. For each feeding bout observed, data were collected on location, habitat type, behavior, group size and composition. The species of plant consumed, plant part consumed, and maturity of fruits were recorded. Samples of plants consumed were collected after macaws left the area and were identified by expert botanists.

Data on independent foraging events from January 2004 to January 2008 were analyzed to characterize macaw diet. Each feeding bout was considered a single observation, regardless of the time spent feeding at that site or number of individuals observed. A total of 810 independent foraging events were recorded, with 463, 187, and 160 being recorded for *A. ararauna*, A. *chloropterus* and *A. macao* respectively. Plant items consumed were categorized by (1) species or genus, (2) plant part: fruit, leaf, bark, flower, other, by (3) reproductive part: pulp, pericarp, entire fruit, seed only, and (4) maturity: immature, mature. Seasons were divided by dry season (May 15-October 14) and wet season (Oct 15-May 14).

A total of 839 foraging trees were tagged and monitored from February 2005-December 2006 which represent 139 species used by all focal animals of the study. Based on methodology by Fournier (1974) a value of 0 to 5 was assigned to each tagged tree, with 5 representing 100% of a maximum load for each reproductive part (bud, flower, immature fruit, mature fruit, dry fruit) at the time of observation. The values of approximately two years of phenology data were averaged to a single annual cycle. A subset of 35 species of trees used by macaws for foraging was selected for subsequent analyses. All tree species were equally accessible to all macaw species.

Nesting trees

Suspected nesting trees were monitored until the status of that nest was confirmed (establishment, incubation, nestlings, or not-active). Suspected and confirmed nests were identified to species, recorded with a GPS, and monitored subsequent years. Confirmed nests were observed monthly, for 6 hour periods, to monitor any change in status during the nesting season until the young fledged or the nest failed.

Data analysis

Three sets of data were used for the dietary analysis (Table 18). Diversity and niche measures for marked and unmarked macaws of each species were calculated for each season (wet and dry), annual selectivity was calculated for the sample of marked macaws, and seasonal selectivity was determined by pooling marked and unmarked individuals for each species. The numbers of foraging events for the selectivity data sets are different from the diversity and niche data sets because only the foraging events consisting of plant species in the phenology database were used.

Table 18
Number of foraging events for each species of macaw used for dietary characterization, diversity, niche and selectivity analyses.

Analysis	*Data set*	*AA*	*AC*	*AM*	*Total*
Diversity, niche breadth and niche overlap	Pooled Dry	227	80	81	388
	Pooled Wet	236	107	79	422
	Total Pooled Events	463	187	160	810
Seasonal selectivity	Total Pooled Events	391	141	105	637
Overall selectivity	Total Marked Events	213	76	21	310
	Total Marked Individuals	13	5	5	23

Diet characterization

The relative frequency of different food items in the diet (fruit, leaf, flower, nectar, other) was calculated for each species for each season. To identify key foraging species for each species of macaw, the relative frequency of observations made for each foraging tree species was generated for the entire year. Key species were defined as those that composed 70% of the foraging observations. I did not categorize key species by season.

Dietary diversity and niche measurements

Several indices were used to characterize dietary diversity for each macaw diet: species richness, dominance, evenness, and diversity. These values were computed using EcoSim (Gotelli and Entsminger 2009). For comparison purposes, uneven sample sizes were equalized by taking a random subsample of 100 feeding bouts for each macaw species for analysis. When diets were further divided into wet and dry season, random subsamples of 50 feeding bouts were used. To determine whether seasonal differences were significant, a 95% confidence interval was generated by EcoSim for each diversity measure. For dietary overlap, significant differences ($\alpha = 0.05$) were determined by comparing observed values with expected values based on Monte Carlos simulations (Dezbiez et al. 2009) which consisted of 1000 iterations using the rarefaction curve option.

Species richness is simply the number of species occurring in the diet. EcoSim calculates this by tabulating the number of non-zero rows in the input variable and in the rarefied samples and generates a 95% confidence interval. The PIE Hurlbert´s index

(1971) was used to calculate evenness, and gives the probability that two randomly sampled food items from the dataset represent two different species. In this equation:

$$PIE = \left[\frac{N}{N-1}\right]\left[1 - \sum_{i}^{s} p_i^2\right]$$

N equals the total number of species in the assemblage, and p_i represents the proportion of the entire sample represented by species *i* ($p_i = N_i/N$). This index ranges from 0 to 1, where 1 represents complete evenness.

Dominance is the proportion of the diet that is represented by the most common species, ranging from no dominance (0) where all species occur at the same frequency to complete dominance (1).

Dietary diversity was measured using the Shannon-Weiner diversity index, where p_i is the proportion of the sample represented by species *i,* and *s* is the number of species:

$$H' = -\sum_{i=1}^{s} p_i \ln p_i$$

Here, the higher the value of H', the higher the probability that the next fruit consumed will not be the same species as the previous one. This index ranges from 0 to 1, with 1 representing the highest amount of diversity.

To determine the degree of dietary overlap among species and between seasons, we used Pianka's index of niche overlap (Pianka, 1973). In this index:

$$O_{jk} = \frac{\sum_i^n p_{ij} p_{ik}}{\sqrt{\sum_i^n (p_{ij}^2)(p_{ik}^2)}}$$

p_{ij} is the proportion of food category i recorded in diet of the species j, and p_{ik} is the proportion of food category i used by species k. *The* O_{jk} index ranges from 0 to 1, with 0 representing no overlap, and 1 representing complete overlap.

In calculating Pianka's overlap using EcoSim, there are four possible choices of randomization algorithms (RA1-RA4) based on whether niche breadth is retained or relaxed (whether the degree of specialization for a given species changes) and whether items not consumed (zero states) are reshuffled or retained. As recommended by Winemiller and Pianka (Winemiller and Pianka 1990) I chose RA3 (niche breadth retained/zero states reshuffled). Since the zero values do not represent constraints other than competition (macaws could have used any of the possible diet items) this was the best option. A "hard zero" was not used to limit availability of diet items, because availability remained equal among all species of macaws when in season.

To determine the degree of diet specialization for each species and season, niche breadth was calculated using the standardized Levin's index (Levins 1968; Colwell and Futuyma 1971; Hurlbert 1978). The Levins index formula is:

$$\mathrm{B} = \frac{1}{\sum_i^n p_i^2}$$

where n is the number of food categories and p is the proportion of records for each food category (i). This was standardized to 1 using the standardized Levins index:

$$\mathrm{B_{sta}} = \frac{(\mathrm{B} - 1)}{(\mathrm{B_{max}} - 1)}$$

where B is Levins index (Levins 1968) and B_{max} total number food categories recognized. In this index, a value of 0 means one resource state is used exclusively (specialization), and a value of 1 means all resources states area used in equal proportions (generalization).

Nest tree diversity and niche measures

Nesting resources of each macaw species were characterized by tree species used and substrate type (live palm, dead palm, live tree, dead trunk). Diversity measures (diversity, richness and dominance) were calculated as well as niche overlap and breadth using the same methodology for the diet data.

Diet selectivity

Although many foraging trees may be producing fruits consumed by macaws, we expect there to be preference for some species over others. To determine whether food preferences exist or whether food consumption is simply a factor of availability, we compared "use" (independent foraging observations) with "availability" of foraging items (abundance indices from phenology data).

I evaluated diet selectivity using Neu's method (Neu et al. 1974), which is one of the most common methods (Alldredge and Ratti 1992) because it is straightforward, interpretable, and appropriate for studies of Design I and II. This flexibility was important because both overall dietary preference of marked individuals (Design II) and seasonal preference at the population level which included unmarked individuals (Design I) were evaluated. A critical assumption for Neu's method is that availability is equal for all individuals. There is no reason to believe that accessibility to resources

differ among individuals or species. Food preferences were analyzed using the program Resource Selection for Windows, written by Fred Leban (Leban 1999). Only plant items for which phenological data existed (n = 41 species) were used, and only foraging data consisting of fruit and flower consumption were used. Foraging observation of flowers containing nectar or water, and leaves and bark were removed from the analysis. If a significant difference between "use" and "availability" was detected, a Bonferroni Z-statistic was used to identify which plant items were used more (preferred) or used less (avoided) than expected. Only plant items that were "preferred" were reported because in the context of this analysis, plant items on the diet list were all consumed by macaws, so they were not actually "avoided". The output also identified plant items which were "preferred" but not significantly "preferred" which were also reported.

To examine overall preference for each species of macaw, the Cumulative Index of Abundance (CIA) was calculated by summing the monthly values of abundance for each plant item (fruit and flower only) and the "availability" of each resource was the proportion that each plant item contributed to the total. "Availability" of each resource was compared to the count of foraging events by each marked individual for each given plant item ("use").

To examine monthly variation in dietary preference, it was necessary modify the study design to Design I (population level) to incorporate foraging observations of unmarked individuals. All individuals (marked and unmarked) were pooled by species, and each temporal period was analyzed independently using Neu's method as described previously. Neu's method ultimately pools individuals together during the processing of

selectivity, making it fairly insensitive to individual variation hence its utility in Design I studies. Other methods explored to incorporate fluctuations in monthly availability had computational limitations.

The datasets for each species of macaw were subdivided into 6 temporal periods: January/March (late wet season), April/May (early dry), June/July (dry), August/September (late dry), October/November (early wet), and December (wet), and each subset was processed independently (Table 19). February was not included due to lack of sufficient phenology data for macaw dietary items. These categories coincide with the breeding (October-May) and non-breeding season (June-September) of macaws. For each temporal period, "use" data consisting of pooled "marked" and "unmarked" individuals and was compared with the "availability" data of plant items in the diet.

Table 19
Number of foraging events of marked and unmarked macaws (use) for each temporal period were compared with the foraging plants "available" for each macaw species (AA = *A. ararauna*, AM = *A. macao*, AC = *A. chloropterus*).

Temporal Period	*AA*	*AC*	*AM*
Jan/Mar	21	18	4
Apr/May	105	26	36
Jun/Jul	49	14	10
Aug/Sep	100	30	29
Oct/Nov	95	44	24
Dec	21	9	2
Total	391	141	105

RESULTS

Dietary characterization

Immature fruits represented greater than 70% and as much as 90% of the fruit items within the diet. The preference of immature fruits was highest in *A. chloropterus* where 91% of the fruits consumed during the wet season were immature, and in dry season immature fruit represented 86% of the fruit consumed (Table 20).

Table 20
Proportion of immature and mature fruit consumed during wet season and dry season by *A. ararauna* (AA), *A. chloropterus* (AC) and *A. macao* (AM).

	Wet season			*Dry season*		
Species	N (fruit)	immature	mature	N (fruit)	immature	mature
AA	205	84.4%	15.6%	170	74.1%	25.9%
AC	95	90.5%	9.5%	63	86.3%	13.7%
AM	63	73.0%	27.0%	61	75.4%	24.6%

When analyzed by reproductive part (entire fruit, seed extraction, pulp only), seeds composed the majority (> 50% and as much as 88%) of the diet for all species for both seasons (Table 21). *Ara chloropterus* was the highest consumer of seeds; extracting the seed for 88% of the fruit items during wet season, and 85% during dry season. Fruit and pulp were consumed at lower frequencies (wet season 8% and 4% respectively; dry season 7% and 8%). *Ara ararauna* consumed 15% and 13% of fruit and pulp during wet season, and 16% and 22% during dry season, with seeds being the remainder of the diet (72% and 62%). *Ara macao* consumed 36% and 9% of fruit and pulp during wet season,

and 13% and 21% during dry season, with seeds being the being the remainder of the diet (55% and 65%).

Table 21
Reproductive parts consumed by macaws (entire fruit, seed only, and pulp only) during wet season and dry season (AA = *A. ararauna*, AC = *A. chloropterus*, AM = *A. macao*).

	Wet season				*Dry season*			
Species	N	fruit	seed	pulp	N	fruit	seed	pulp
AA	208	14.9%	72.1%	13.0%	188	16.0%	62.2%	21.8%
AC	97	8.2%	87.6%	4.1%	74	6.8%	85.1%	8.1%
AM	67	35.8%	55.2%	9.0%	61	13.1%	65.6%	21.3%

Overall diet for all species of macaws consisted of fruit, leaf, flower, nectar and other plant items (bark, insects, etc), with fruits representing over 85% of the diet for all seasons (Fig. 20). For all macaws, consumption of fruit declined in the dry season as higher proportions of flowers, leaves, and nectar were consumed.

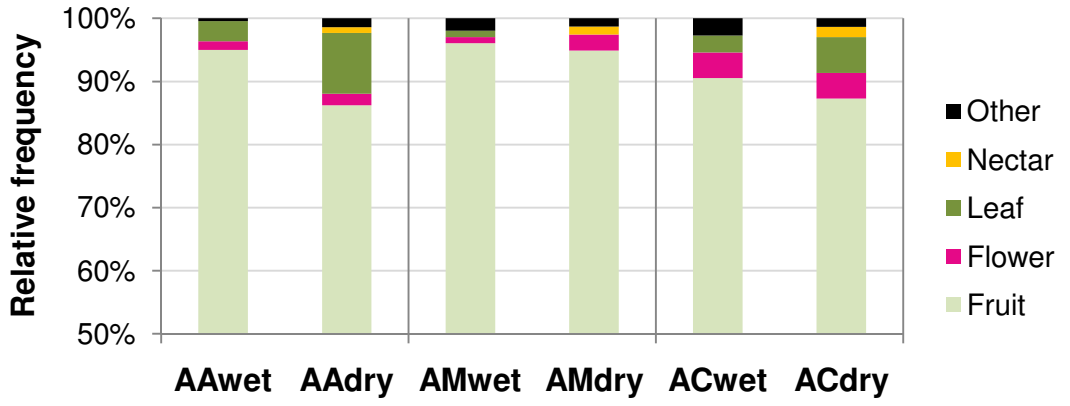

Fig. 20. Relative frequency of food items occurring in the diet of each species of macaw (AA = *A. ararauna*, AM = *A. macao*, AC = *A. chloropterus*) during the wet season and the dry season. During the dry season fruit consumption declines as a greater proportion of flowers, leaves and nectar appear in the diet.

Diet composition (Table 22) during wet season was composed of fruit (94%), flowers (2%), leaves (2%) and other (2%). Dry season diets were composed of fruit (90%), flowers (3%), leaves (5%), nectar (1%) and other (1%). Nectar consumption was observed only in the dry season.

Table 22
Overall composition of dietary items during the wet season and dry season.

Item		*wet*	*SE*	*dry*	*SE*
Fruit		93.9%	1.7%	89.5%	2.7%
	immature	82.6%	5.1%	78.6%	3.9%
	mature	17.4%	5.1%	21.4%	3.9%
Flower		2.1%	1.0%	2.8%	0.7%
Leaf		2.3%	0.7%	5.1%	2.8%
Nectar		0.0%	0.0%	1.3%	0.2%
Other		1.7%	0.7%	1.3%	0.0%

There was seasonal variation in the peaking of plant items throughout the year (Fig. 21). At the commencement of dry season (May), the load of immature fruit (n = 31 species) increased steadily throughout the year until the middle of wet season (Nov-Dec) where it decreased during January and February. From February through April (the latter part of wet season), mature fruit (n = 30 species) peaked, and by dry season, had decreased and remained constant the remainder of the year. Flower (n = 27 species) loads remained constant throughout the year. From May through January, immature fruits were the most abundant plant item available, whereas from February through April, mature fruits were the most abundant.

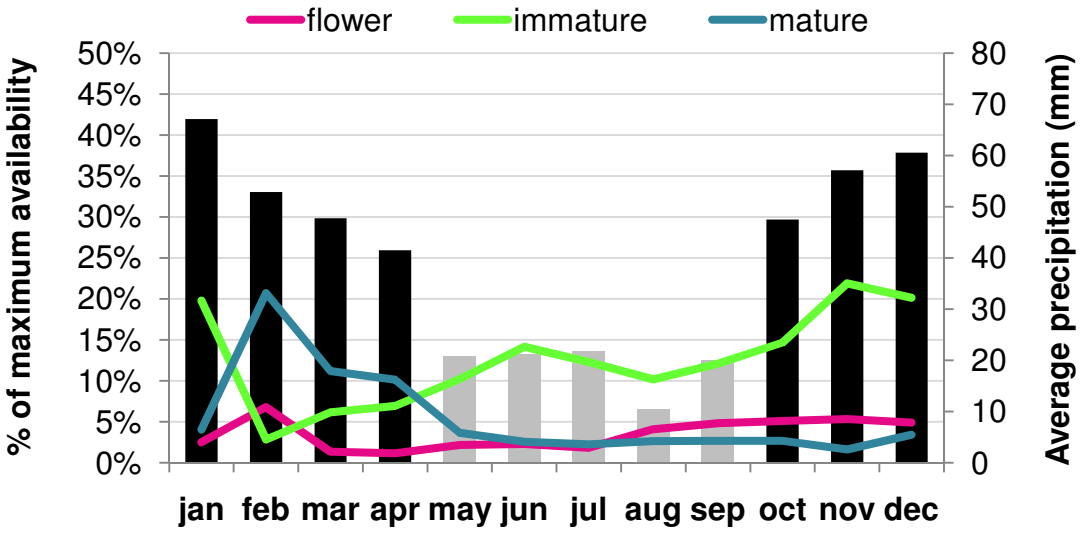

Fig. 21. Monthly availability of plant items used by macaws (source: phenology data), showing seasonal variation in precipitation, with black bars representing wet season, and grey bars representing dry season (source: Los Amigos weather station 2004-2008).

Annual diets for each species were very broad, with > 200 species being documented, representing at least one single foraging event of a unique species. Of these, 130 specimens were collected for identification and photographic documentation, and 101 were identified (n = 91) or given a unique code (n = 10). Of these 101 species,

18 plants were shared by all macaws, and 49 plants were shared by 2 species of macaws, and 36 plants were used by only one of the three species of macaw (Appendix A).

Several observations were made for some of the key species (Table 23) consumed by each species of macaw that indicated behavioral and perhaps morphological differences. Palm species were either consumed exclusively or at greater frequency by *A. ararauna*, which also roosted and nested in palm swamps. Foraging observations in palms were not restricted to palm swamps, and ocurred frequently within upland forest which was shared by all species of macaws. *Ara macao* consumed hard fruits that were small or large, but not of medium size. *Ara macao* tended to be more precise at opening difficult fruit, working with the structural weak points of the fruit. Although *A. macao* lacked the physical strength of *A. chloropterus* to pierce a hole in the thick woody shell of Brazil nut, it was still a significant component of the diet of *A. macao*. Perhaps hard fruit of a medium size were difficult to manipulate to strategically open them using their toes and beaks.

Table 23
These plants made up > 70% of the annual diet for each macaw species. Each percentage is the contribution of each given plant species to the overall diet. (AA = *A. ararauna*, AC = *A. chloropterus*, AM= *A. macao*)

Species	*AA*	*AC*	*AM*
Bertholletia excelsa	13.8%	28.3%	6.9%
Hevea guianensis	10.8%	6.4%	-
Iriartea deltoidea	**9.1%**	1.1%	2.5%
Mauritia flexuosa	**6.9%**	2.1%	3.1%
Parkia A39	5.2%	5.3%	1.3%
Swartzia A176	5.0%	1.1%	1.3%
Cecropia schyadophylla cf	4.1%	1.1%	0.6%
Euterpe precatoria	**3.9%**	1.1%	5.0%
Sloanea rufa cf	3.2%	1.1%	1.9%
Dipterix micrantha	1.7%	1.1%	-
Inga A47	1.7%	1.6%	<1%
Pseudolmedia laevis	1.7%	<1%	**3.8%**
Socratea exorrhiza	**1.7%**	-	-
Castilla ulei cf	1.5%	-	**2.5%**
Eschweilera A18	1.5%	2.1%	1.9%
Jacaranda copaia	<1%	4.3%	1.3%
Cariniana decandra	-	3.2%	4.4%
Byttneria pescapraefolia	<1%	2.7%	1.9%
Apeiba membranacea	<1%	2.7%	1.3%
Hura crepitans	-	2.1%	-
Caryocar amigdaleiforme	-	1.6%	<1%
Terminalia oblonga	<1%	1.6%	-
Gurania A25	<1%	1.1%	2.5%
Pouteria A73	<1%	1.1%	2.5%
Manioc leptotilla	-	1.1%	1.3%
Couratari guianensis	-	<1%	5.6%
Erithrena poephiana	<1%	<1%	**1.9%**
Symphonia globulifera	<1%	-	**3.8%**
Phyllocarpus riedelii	<1%	-	3.1%
Sapium glandulosum cf	-	-	3.1%
Couepia A152	-	-	2.5%
Cayoponia A119	-	-	1.9%
Pseudolmedia laevigata	-	-	1.9%
Enterolobium barnebianum	<1%	-	1.3%

All species of macaws consumed *Bertholletia excelsa* (Brazil nut) each month that immature fruits were available (Fig. 22). The fruits were immature during February,

March and April, however there did not appear to be any temporal partitioning among species of this hard fruit, which may have ocurred for the weaker-mandibled *A. macao.*

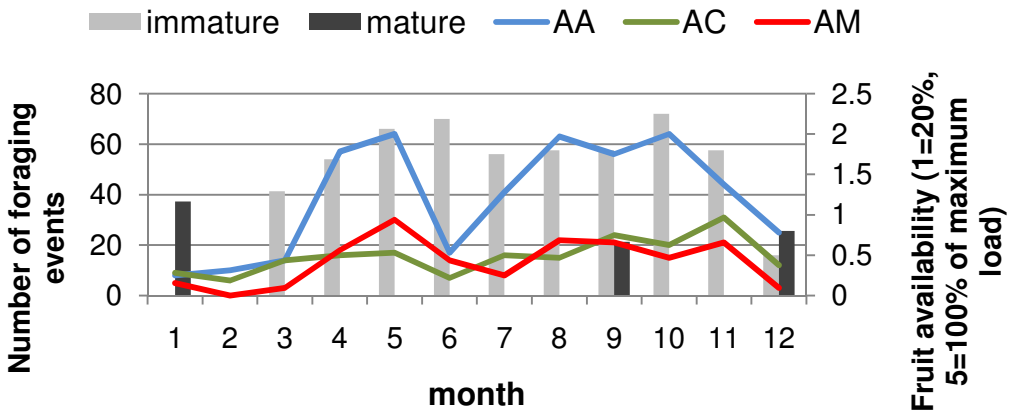

Fig. 22. Monthly consumption of Brazil nut (*Bertholletia excelsa*) by each species of macaw, showing the availability of immature (grey bars) and mature (black bars) fruits each month (scale of 0 to 5, with 5 representing maximum fruit load (100%).

Dietary diversity and niche measurements

Species diversity and richness in macaw species' diets was slightly greater in dry season than wet season (Table 24), and based on the 95% confidence intervals, both diversity and richness were significantly greater for *A. chloropterus and A. macao*. The diversity and richness of the diet of *A. macao* was significantly greater than *A. chloropterus* and *A. ararauna* during the wet season, and during the dry season only dietary diversity of *A. macao* was significantly greater than *A. chloropterus* and *A. ararauna. S*pecies evenness was highly uniform for each diet (close to 1.0), with *A. macao* exhibiting the greatest amount of evenness each season. Seasonal difference in evenness was only significant for *A. chloropterus,* which showed an increase in evenness

during the dry season. Dominance (heterogeneity) of the diet overall was fairly low (ranging from 0.09 to 0.38) for both seasons, and least for *A. macao*, and greatest for *A. chloropterus*. Dominance was greatest during wet season for all macaws, but only significantly greater for *A. chloropterus*.

Table 24
Diversity of plant species in macaw diets during the wet season and dry season. Diversity measures were calculated from a random sample of 50 foraging events for each macaw species. Observed foraging events for AA, AC, AM during wet season were 217, 98, 70, and during dry season were 217, 76 and 71 respectively.

	Wet season				*Dry season*			
Species	Richness	Dominance	Evenness	Diversity	Richness	Dominance	Evenness	Diversity
AA	**20**	**0.23**	**0.9**	**2.55**	**22**	**0.15**	**0.94**	**2.83**
95% CI	15-25	0.16-0.30	0.85- 0.94	2.21-2.83	18-26	0.10-0.20	0.92-0.96	2.60-3.05
AC	**19**	**0.38**	**0.84**	**2.32**	**26**	**0.21**	**0.94**	**2.93**
95% CI	15-23	0.28-0.48	0.77-0.90	2.03-2.59	23-30	0.14-0.26	0.91-0.96	2.72-3.13
AM	**28**	**0.14**	**0.96**	**3.1**	**29**	**0.09**	**0.97**	**3.21**
95% CI	24-31	0.10-0.18	0.95-0.97	2.94-3.25	26-32	0.08-0.12	0.96-0.98	3.07-3.34

Observed dietary overlap (Table 25) among all species during both seasons was higher than expected based on simulated means ($p < 0.05$ for all calculated indices). The degree of overlap between macaw species was higher in the wet season (ranging from 0.61 to 0.81) than the dry season (ranging from 0.30 to 0.58). *Ara ararauna* and *A. chloropterus* had the highest degree of dietary overlap, which may be explained by their strong preference for similar foods that *A. macao* either did not consume or did not prefer. There was less dietary overlap during dry season for all macaws, which would be expected if diets diversified from the inclusion of alternative food items, yet these food items were not shared among macaw species.

Table 25
Mean dietary overlap (Pianka's index) among species was significantly greater than expected (p = 0) in each season, and overall was greater in the wet season than the dry season.

Overlap	*Wet season*	*Dry season*
AA:AC	0.805355	0.575521
AA:AM	0.607514	0.331699
AC:AM	0.664137	0.299862
Mean Overlap	0.69234 (p = 0)	0.40236 (p = 0)
Variance	0.01038 (p = 0.21)	0.02274 (p = 0.07)

Dietary breadth which was measured by Levin's Standardized Index (Table 26) was greatest for *A. macao* in both seasons (wet 0.55, dry 0.69) which suggested this species is more generalized than *A. ararauna* (wet 0.21, dry 0.37) and *A. chloropterus* (wet 0.19, dry 0.38). The diet was more generalized during the dry season for all species of macaws.

Table 26
Niche breadth of wet season and dry season diets for each species of macaw (AA = *A. ararauna*, AC = *A. chloropterus*, AM = *A. macao*).

BA (Levin's Standardized Index)	*Wet season*	*Dry season*
AA	0.21428	0.365765
AC	0.18568	0.376744
AM	0.54522	0.686843

Nest tree diversity and niche measurements

Nesting substrate richness (dead palm, live palm, live tree, and dead trunk) was greatest for *A. macao* which used all four substrate types for nesting (Fig. 23). *Ara chloropterus* and *A. ararauna* used only 2 substrate types, and *A. chloropterus* nested 95% of the time in live trees, and *A. ararauna* nested 99% of the time in dead palms.

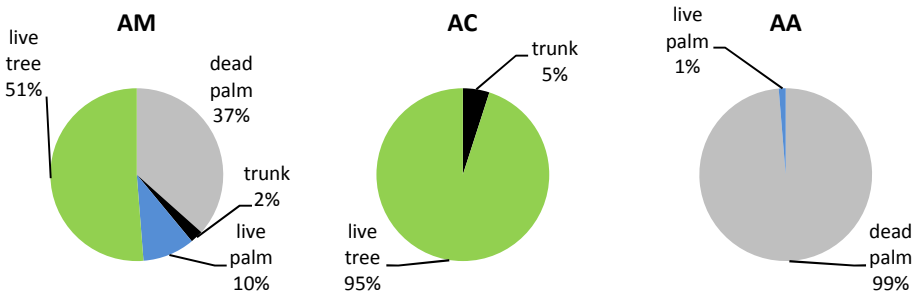

Fig. 23. Substrate types used for nesting (n = 139 nests observed, including unconfirmed nests) by each species of macaw recorded from 2004 to 2008.

Of 139 potential nests (cavities where macaws exhibited nesting behavior such as establishing or remaining inside) 90 cavities were confirmed as active nests (incubation and/or nestlings) (Table 27). *Ara macao* used the greatest number of species (6 species nested, 8 species explored), whereas *A. chloropterus* nested almost exclusively in a canopy emergent *Dipterix micrantha*, and *A. ararauna* almost exclusively in dead *Mauritia flexuosa* palms (common name = “aguaje”).

Table 27
List of tree species used by macaws for nesting (between 2004 and 2008), which shows the total number of cavities associated with nesting behavior, and confirmed nests (incubation and/or nestlings established). For each species of macaw, the number of confirmed nests as well as its relative frequency (%) is given for each tree species.

Nest Tree Species	*Total*	*Confirmed*	*AM*	*AC*	*AA*
Mauritia flexuosa	81	58	3 (17.6%)	-	55 (96.5%)
Iriartea deltoidea	16	8	6 (35.3%)	-	2 (3.5%)
Dipterix micrantha	28	17	4 (23.5%)	13 (81.3%)	-
Capirona decorticans	4	3	2 (11.8%)	1 (6.3%)	-
Apuleia leiocarpa	1	1	-	1 (6.3%)	-
Cariniana sp	2	1	1 (5.9%)	-	-
Ceiba sp	1	1	1 (5.9%)	-	-
Parkia sp	1	1	-	1 (6.3%)	-
Cedrelinga cateniformis	2	0	0 (0%)	-	-
Erithrena poephiana	3	0	0 (0%)	-	-
Total	**139**	**90**	**17 (100%)**	**16 (100%)**	**57 (100%)**

Ara macao exhibited the highest diversity of nest trees (1.56), the lowest dominance (0.35) and 95% of the time used between 5-6 tree species (Table 28). In contrast, *A. ararauna* exhibited the lowest diversity (0.13) and greatest dominance (0.97). Intermediate of the three species was *A. chloropterus* with a nest tree diversity of 0.68, species richness of 4 (95% of the time expected to nest in 3-4 species) yet dominance was fairly high (0.81) due to the high frequency of *Dipterix micrantha* as a nesting tree. The degree of specialization (niche breadth) was greatest for *A. ararauna* (0.07) which agreed with their almost exclusive use of the dead "aguaje" palm (*Mauritia flexuosa)*, and *A. macao* were generalists both for species (0.66) and substrate type, as seen by substrate richness previously (AM = 6, AA and AC = 2). *Ara chloropterus* and *A. ararauna* did not have any overlap in nesting trees (Pianka's Overlap Index = 0),

whereas *A. chloropterus* and *A. macao* had the highest amount of overlap (0.503) and *A. ararauna* and *A. macao* were intermediary (0.393) due to *A. macao* using species (and substrates) common to both *A. ararauna* and *A. chloropterus. Ara macao* nested in cavities that *A. chloropterus* do not nest in (KA pers. obs.), and very rarely nested in dead palms occurring in nesting swamp habitat of *A. ararauna*.

Table 28
Diversity and niche breadth measures of nesting tree species used by macaws between 2004 and 2008 demonstrate that *A. macao* had a significantly more generalized nesting strategy, using more species and substrate types than *A. chloropterus* and *A. ararauna*.

Measure	*AM*	*AC*	*AA*
diversity	1.56	0.68	0.13
95% CI	1.40-1.66	0.49-0.72	0.00-0.39
richness	6	4	1
95% CI	5-6	3-4	1-2
dominance	0.35	0.81	0.97
95% CI	0.27-0.40	0.80-0.87	0.87-1.0
Niche Breadth	0.662687	0.162791	0.072631

Dietary preferences

Of the 41 species of plants consumed by macaws of which phenology data existed, *Bertholletia excelsa* (Brazil nut), consumed as an immature fruit, was the dominant food preferred by *A. ararauna* and *A. chloropterus* ($p < 0.05$) in the overall selectivity analysis. In the previously listed foraging observations (Table 23), this is the food item that occurred at greatest frequency for all three species of macaws, and was consumed at a greater frequency than expected compared to its availability. This tree species was also the most frequently occurring item in the diet of *A. macao*, but not

significantly preferred. In addition to *Bertholletia excelsa, A. ararauna* also showed a significant overall preference for *Hevea guianensis* ("rubber tree") and *Swartzia sp.*

When examined seasonally, several more dietary preferences were revealed (Table 29). In addition to *Bertholletia excelsa*, *Hevea guianensis* and *Swartzia sp.* were important dietary species for *A. chloropterus* also. Interestingly, *Bertholletia excelsa* and *Hevea guianensis,* which had the hardest pericarps, were not preferred by *A. macao*. *Bertholletia excelsa* was consumed when immature by all species, yet *Hevea guianensis* was not consumed at all by *A. macao.*

Table 29
Dietary preferences for macaws throughout the year.

Species	Jan/Mar	Apr/May	Jun/Jul	Aug/Sep	Oct/Nov	Dec
AA	*Hevea guianensis*	*Bertholletia excelsa*	*Hevea guianensis* *Swartzia sp.* *Tachigali sp.*	*Parkia A39* *Sloanea sp.* *Swartzia sp.*	*Hevea guianensis*	*Hevea guianensis* *Pouteria*
AC	*Hevea guianensis*	*Bertholletia excelsa*	-	*Swartzia sp*	*Bertholletia excelsa*	-
AM	-	*Euterpe precatoria*	-	*Couratari sp.* *Swartzia sp.*	-	-

It is important to note that there were several species of plants that should be considered significant contributors to the diet of macaws despite their absence in the selectivity analysis. *Inga* species (family Fabaceae) are numerous and occurred

frequently in the diets of all macaws most notably during the dry season, yet this genus is so speciose (> 100 species in Los Amigos) that botanical identification is still ongoing. Although two species were included in the phenology study, macaws actually consumed more than two species. Similarly, *Cecropia* and *Pseudolmedia* species (Sep/Oct/Nov), as well as *Castilla sp.* (Aug/Sep/Oct) are also important at certain times of the year. Interestingly, *Pseudolmedia* (n = 3 species) and *Castilla* species are the only species consumed in their mature state. When these species are abundant, the probability that a macaw will be found eating these species is extremely high, but unfortunately there are no data to demonstrate this.

From this analysis, *A. macao* did not appear to have much preference, which could be attributed to a smaller sample size. However, *A. macao* are also the most generalized species in terms of diet breadth and richness and as generalists, it would not be unexpected that strong preferences were not exhibited.

DISCUSSION

Seasonal variation in diet composition was exhibited by all three species of macaws, but there was little evidence of competition for food resources. Several tree species important for nesting and foraging were revealed, and in particular, palm habitat was a key resource for *Ara ararauna*.

Competition over food resources

As seed predators of a resource which few frugivores are able to consume due to the mechanical and chemical restraints and location in the canopy, it is reasonable to question whether competition existed between these co-existing species. Immature fruit composed over 70% of the diet for all species in the wet season and the dry season. However, the vast number of plant species consumed by macaws may provide enough foraging opportunities that partitioning may not be necessary. Furthermore, overlap values among macaws for either season were less than 0.7, which is a general rule of thumb for potential competition. Phenology data showed that immature fruit were the most abundant food item in the forest canopy, with the exception of February and March when mature fruit were more abundant. During these months, *Hevea guianensis*, *Cariniana sp*., and *Jacaranda sp*. which were at their peak production were heavily consumed. In over three years of observation, the highest level of interspecific aggression was one macaw displacing another on a branch, yet both remained in the

same tree, suggesting that food resources may not be a limiting resource. This is not unexpected, due to the large extent of still intact habitat in the immediate study area.

Dietary characterization and specialization

Macaws are generally thought to have a narrow dietary breadth and to use only a small proportion of available food resources throughout the year (Inigo-Elias 1996; Loza 1997; Contreras-González et al. 2009). Dietary breadth of psittacids has been explored for species occurring from the dry forests of Mexico to the tropical wet forests of South America (Renton 2006; Contreras-González et al. 2009; Matuzak et al. 2009). For *A. macao*, dietary breadth, measured by the standardized Levin's niche breadth index (B), was reported to be 0.216 and 0.139 in wet and dry season of western Costa Rica (Matuzak et al. 2009), and 0.394 during the dry season in southwestern Belize (Renton 2006), whereas in the dry tropical forest of central Mexico, *A. militaris* (Military macaw) had a wet and dry season dietary breadth of 0.033 and 0.158 respectively (Contreras-González et al. 2009); all of which have relatively small values on a scale of 0 (specialist) to 1 (generalist).

This is the first time that dietary breadth for *A. ararauna* and *A. chloropterus* is reported, and it is comparable to the other species of large macaws reported in the literature. Wet and dry season dietary breadths are narrow; ranging from 0.214 and 0.366 for *A. ararauna* and 0.186 and 0.377 for *A. chloropterus*. In contrast, the diet of *A. macao* is twice as broad than what is reported elsewhere (wet season 0.545 and dry 0.687) and by definition, *A. macao* should be considered a generalist in this study area.

Higher values of dietary breadth (0.5 to 0.75) have been reported for smaller bodied parakeets, parrots, and Amazons (Sosa-Asanza 2000; Renton 2006). Large body size requires greater protein content for maintenance (Sakai et al. 1986; Koutsos et al. 2009) as well as lipids for breeding and nestling growth (Vriends 1991). The proportion of seeds in the diet, which are the most nutritious part of the plant (Gilardi 1996) were positively correlated with large body size in a parrot community in Costa Rica, and pulp (fruits) were correlated with smaller body size. Flowers and leaves, which are generally higher in other nutrients such as carbohydrates, minerals, and water (Gilardi 1996) were not correlated with body size (Matuzak et al. 2009).

What might explain the large dietary breadth of *A. macao* that is greater than smaller bodied psittacids and so different from the expected values that *A. ararauna* and *A. chloropterus* have? After comparing the characteristics of the items consumed by each species, I observed that a large proportion of *A. macao*'s diet consisted of smaller fruit and larger fruit, but medium-sized fruit with hard pericarps did not occur as frequently. The precision by which *A. macao* would manipulate large hard fruit was notably different from the other species, which leads me to speculate that medium-sized hard fruit may be difficult to manipulate, and that *A. macao* lack the strength to crush it. *Ara macao* are slightly heavier than *A. ararauna*, yet their mandibles may be weaker, driving them to incorporate smaller and nutritionally less energetic (Van Schaik et al. 1993; Fenner 1998) items in their diet. *Ara ararauna* may have evolved stronger mandibles due to the excavation that is commonly necessary for preparing a nest cavity. In Costa Rica, *Ara ambiguus* is the only species, other than the mammalian agouti, that

has specialized mouth parts able to pry open the extremely hard fruits of *Dipteryx panamensis* on which it depends on for 6 months of the year. In contrast, *A. macao* which co-exists with *A. ambigua* did not consume these hard seeds (G. Powell pers. comm.; KA pers. obs.).

Another possible explanation for the significantly broader diet for *A. macao* in this study compared to *A. macao* of other studies may be attributed to a combination of factors such as geographic location, habitat history and length or season of study. Not only did these studies originate from different countries, they range from dry to wet ecoregions where plant diversity and abundance differ. In the dry tropical forest and oak forests of central Mexico, only 10 species of plants over 12 months of study were observed to be consumed by *A. macao* (Contreras-González et al. 2009), and in western Ecuador, *A. ambiguus* consumed 9 species in 2 years, which were determined to comprise the majority of species in a region heavily impacted by deforestation (Berg et al. 2007). The population of *A. macao* in central Mexico consumed 12 species, but focused on only 2 species (Renton 2006), and this study was only 3 months over the breeding season. Similarly, in the southern pacific of Costa Rica, although the sample size and study length were significantly greater (600 foraging bouts over 2 years) the hand-raised and re-introduced *A. macao* consumed 32 species, and of these 76% were non-native species; although this reflects their ability to adapt, the narrow diet breadth may be a reflection of lack of training and knowledge of available resources (Matuzak et al. 2009). In central pacific Costa Rica, *A. macao* were opportunistically seen to feed from 43 species over a four year period (Vaughan et al. 2006a) in a region where greater

than 90% of the habitat has been altered. In the Peruvian Amazonian rainforest, 52 species of plants were consumed by *A. macao* in Manu (Gilardi 1996) in a region with comparable species richness and composition to my study area. Considering the large number of plant species, it is doubtful that this is a complete list of dietary items. In the same study area (Munn 1988), 38 species were reported to be consumed by *A. macao*, but considering that only 1 species was reported for each of *A. manilata* and *A. militaris*, and 11 for *A. severa*, it is apparent that sampling effort is also a factor in accurately determining dietary range. *Ara macao* however, did consume more species than *A. ararauna* (20) and *A. chloropterus* (16), which is consistent with the pattern seen in this study as well. In comparison, this study of four years resulted in greater than 100 plant species for macaw species individually, and for the three co-existing macaw species, greater than 200 plant species were used as food resources.

Although species richness is not equivalent to dietary breadth, if the species list is incomplete, upon which dietary breadth is calculated, or sample size is small, then the proportions of each item will not be adequately calculated to give an accurate description of the degree of specialization.

The longer the study is the greater probability that the full range of dietary items consumed is sampled. A study limited to a few months ignores dietary items that become available in other months. Similarly, annual cycles vary, and for morphological or physiological reasons, not all plants produce fruit each year. Plant species richness in each area was unknown, so the assumption that macaws consume a small proportion of

available food resources may be site and species specific and should not be applied to all macaws.

If availability is correlated with diet breadth (Wermundsen 1997; Renton 2001) then it would be expected that macaws in this region of high plant diversity and intact habitat would have a higher diet breadth. However, this pattern was only observed for *A. macao*. This might suggest that *A. ararauna* and *A. chloropterus* are actually more specialized within this rainforest habitat.

Seasonal dietary differences

Changes in dietary breadth across seasons have been attributed to seasonal changes in food availability. Several authors speculate that narrow dietary breadth for parrots during the dry season (Gilardi and Munn 1998; Renton 2001, 2006) is due to food scarcity. This often-cited "dry season scarcity" however, is derived from an often-quoted mammalian study (Janson and Emmons 1990) based on fleshy ripe fruit production and plant species which are not specific to macaws. This assumption also fails to consider that macaws mainly consume seeds and fruits of immature reproductive parts (Kinzey and Norconk 1990; Kinzey and Norconk 1993) which have different times of availability than mature fruit. Dry season has also been associated with peak fruit abundance in other studies as well (Contreras-González et al. 2009; Matuzak et al. 2009), and furthermore, the period of peak fruit abundance can be several months different from the period of peak of edible biomass (EBM) (Berg et al. 2007).

Examination of seasonal dietary differences should be associated with the plant parts actually consumed by macaws.

Other studies report a narrower dietary breadth during the dry season (Gilardi and Munn 1998; Renton 2001, 2006) attributing it to food scarcity, however, in this study dietary breadth was greater in the dry season. Considering food resources consume macaw are abundant in the dry season, this result was expected. Not expected, however, was that dietary overlap was less in the dry season. Under the original assumption that dry season was a time of food scarcity, it would be expected that co-existing species would minimize competition by partitioning the resources, thus overlap would be less in the dry season. This study however, produced results expected under the assumption of food scarcity when there was in fact no food scarcity. There was no indication of competition over food resources among macaw species or between macaws and other frugivores either because the principal food source is immature fruits which other animals cannot consume due to mechanical difficulties with opening the hard fruit, the location in the canopy, and toxicity. How then, can a decrease in dietary overlap among non-competing species, when resources are abundant, be explained?

Resource partitioning can occur in the absence of competition (Gordon and Illius 1989). It may occur in the presence of other factors such as predation, or be a differential response to the environment (Schoener et al. 1986), or due to differences in some aspect an animal's traits (Macarthur and Levins 1967; Chase 2005). Predation is low to none and macaws were equally exposed to any environmental gradients if they existed at that scale, so behavioral differences may be the most promising explanation.

When niche breadth, overlap, diversity and preferences are evaluated together, the results which were initially counter-intuitive become more clarified. In the dry season when immature fruit becomes increasingly more abundant, niche breadth increases and niche overlap decreases (resource partitioning increases). This essentially means that each macaw species is incorporating more items into their diet, yet different items from the other species. This is supported by the fact that diversity and richness increased during the dry season, and more flowers, leaves, bark and nectar were consumed in the dry season. During the dry season, there were also a greater number of preferred foods, and during the wet season heavy consumption of fewer preferred foods was reflected by the narrower niche breadth which indicates dietary specialization. The heavy consumption of few preferred species was reflected by greater dominance in the wet season. Thus, differences in food preferences, not scarcity or competition may better explain the broadening and differential divergence of diets during the dry season.

Differential behavioral responses to the environment may also play an important role in seasonal dietary changes. Preferences may be related to subtle differences in beak morphology and ability to consume different food types as discussed earlier. The higher protein and lipid requirements during the breeding season are no longer required in the dry season, “freeing” individuals to exploit a greater variety of different resources. Smaller-bodied psittacids have a metabolism which enables them to be more active in the hotter hours of the dry season (Gilardi and Munn 1998), and their diet which contains more carbohydrates (flowers, leaves, fruits) is sufficient for their smaller bodies to maintain longer periods of activity. Perhaps subtle differences in metabolic

requirements related to body size, and different methods to acquire the macronutrients they need may also account for diversification of diets during the dry season.

Dry season may not be a season of food scarcity for macaws, but it may be a season of water scarcity due to evaporation of watering cavities, and seasonal changes in metabolic requirements due to increased temperatures. For all macaws, flower, leaf, water, "other", and nectar consumption was greater during the dry season than during the wet season. Flower production is fairly constant throughout the year, and leaves (mainly from palm fronds) are also present throughout the year. The behavior of consuming or tipping flowers, or masticating leaves to extract the juices (which consist of principally water and carbohydrates) occurred almost exclusively during the dry season. Of these behaviors, *A. ararauna*, was observed to masticate palm leaves daily, *A. macao* was observed only a few times, and *A. chloropterus* was never observed. *Ara macao* had the highest consumption rate of flowers and nectar. *Ara chloropterus*, which has the strongest mandibles, was most likely to tear off pieces of trunk, the "other" category, to consume what was underneath. Insects and grubs may offer the higher protein and lipid content that the larger *A. chloropterus* requires (Renton 2006).

Peak activity for macaws is in the morning and late afternoon (Snyder et al. 1987; Gilardi and Munn 1998; Burger and Gochfeld 2003; Vaughan et al. 2006a) which suggests that midday heat may affect macaws even during the wet season, and this midday lull has been more associated with warmer months (Westcott and Cockburn 1988; Emison et al. 1994). Macaws do appear to be affected by extreme temperatures: spending more time lower in the canopy in shaded branches in the hotter seasons, and

notably less active in the cold “friajes”. These behaviors, observed frequently during the dry season, suggest a necessity for additional sources of liquid, and the method by which each species acquires these resources varies by species.

Mastication of palm leaves by *A. ararauna* in the areas where they migrated to in the early morning, and before roosting was a behavior rarely seen during the wet season, and certainly never at this intensity. It couldn’t be ascertained whether this behavior was continuous throughout the dry season and exhibited in regions where accessibility was impossible, however, given the strong relationship between macaw movements and palm habitat distribution, it is highly probably that this behavior occurs elsewhere with other populations as well.

Key nesting and foraging resources

The majority of the ecologically valuable tree species used by macaws for food and nesting resources are also economically valuable. *Mauritia* palms, used by *A. ararauna* for nesting and foraging, are known as “aguaje” locally. These palms are valued for the high nutrient content of the fruit and are the most commercially important fruit in the Amazon (Padoch 1988; Peters et al. 1989) and are important source of income for many communities (Peters et al. 1989; Vasquez and Gentry 1989; Kvist et al. 2001; Brightsmith 2005). The traditional method for obtaining the fruit (cutting down the palm) has lead to the destruction of a palm swamps because in the absence of female palms, the swamp habitat did not regenerate (KA pers. obs.).

Dipterix micrantha, a preferred nesting tree for the largest bodied macaw, *A. chloropterus*, is also valuable as a hardwood for construction. This large canopy emergent was also listed as the most important tree for *A. chloropterus* and *A. macao* (Brightsmith 2005), and because it can provide re-useable cavities for over 1000 years (Chambers et al. 1998) it is invaluable to the long-term reproductive viability of many populations of secondary cavity nesting birds. This tree is also considered a keystone species for its fruit (Emmons 1984; Forget 1993; Romo 1997; Powell et al. 1999). The wide-spread land conversion and rapid removal of a close relative (*Dipterix panamensis*) once logging saws were able to cut through the dense trunks, was the single leading cause of the population decline of the Great Green Macaw (*Ara ambiguus*) in Costa Rica, which as a result is now an endangered species. For six months during the nesting season, *Dipterix* was over 90% of the diet, and also the only tree species these specialists nested in (Arias et al. 2000). The diet of *A. chloropterus*, and *A. macao* here is much broader, but their nesting habitat may be threatened if *Dipterix* is not harvested sustainably, keeping into consideration that natural cavities may take several hundred years to form (Brightsmith 2005).

Bertholletia excelsa or Brazil nut (known locally as "castaña") is the most frequently consumed food by all three species of macaws, with the greatest consumption occurring pre-nesting and post-nesting, providing high quality food at critical periods of the year. Brazil nut trees have a fairly restricted range in the Amazon (Peres et al. 2003) and the study area is within the southwestern edge of its distribution range. Brazil nuts are collected once they have matured and fallen to the ground, thus the trees themselves

are not harvested (Taylor 1999). Macaws consume immature fruits (Trivedi et al. 2004) thus they are seen as a pest to Brazil nut concession owners and are sometimes shot (Ortiz 1995). Macaws were estimated to reduce the Brazil nut crop by 10% (Trivedi et al. 2004), but the impact of hunting on macaw populations is difficult to measure, and may increase if market prices continue to plunge.

Hevea guianensis ("shiringa") is a highly selected food by macaws during several months of the year, and is also the species famous for the "rubber boom" in the early 1900's. The latex of this species contains a cyanide-compound that is toxic to many animals (Kongsawadworakula et al. 2009), yet macaws are able to consume the seeds, which are also toxic, in vast quantities. Members of the Lecythidaceae family, of which Brazil nut also belongs to, are important timber products and important food items (*Cariniana sp., Couratari sp., Eschweileira sp*) as well.

Broader implications

Although floodplain habitat is disproportionately important relative to its small area on the landscape for nesting and foraging for all species of macaws, the areas adjacent and beyond these habitats may be just as important for maintaining viable populations (Renton 2004). As the frontier of colonization pushes further into remote areas, bringing along greater infrastructure and technology, the existing large tracks of rainforest, remaining because of inaccessibility will be impacted. The landscape is changing, yet what the outcome will be, and how macaw populations will respond to these changes decades from now cannot be known.

CHAPTER III

SUMMARY AND CONCLUSIONS

Space use and resource use varies among macaw species, individuals, and by temporal period. *Ara macao* and *A. chloropterus* have very similar diets and nesting substrates, but differ in the degree of preference; *A. macao* being more of a generalist, and *A. chloropterus* more a specialist. The diet of *A. ararauna* is very similar to its relatives; however, nesting preferences, movement patterns, and social behaviors are markedly different. Large-scale movements, which were exhibited by all species, are most likely explained by whether a nest is being established or maintained, and unlikely related to food scarcity.

Over the dry season, which corresponds to non-breeding season, there is a change in diet composition, but immature fruit which comprises the bulk of the diet, is the most abundant food item in the canopy. The incorporation of more nectar, flowers, and leaves may be a physiological response to the increased temperatures during the dry season and reduced water availability in the drinking cavities, rather than a response to minimize competition among ecologically similar species.

Long-distance movements out of their ranges by individuals of *A. macao* and *A. chloropterus* with established nesting cavities were observed infrequently and for brief periods. Nest cavity fidelity is extremely high, and even *A. ararauna* re-used the same dead palm if it was still standing. The short life-span of nesting palms for *A. ararauna* may allow them to migrate during the non-breeding season. Breeding individuals

monitored in this research maintained home ranges. Non-breeding individuals, of which only *A. chloropterus* was monitored did not maintain stable ranges. Given that the majority of the population does not breed, there must be a substantial number of transients, or residents looking for nesting opportunities which are limited.

This mobile sector of the population may explain the seasonal fluctuations in abundance observed by other researchers. The degree to which these individuals may be tracking resources across the landscape as they become available is unknown. However, if the large-scale seasonal migrations of *A. ararauna* and non-breeding *A. chloropterus* are any indication of the size of area used, it is reasonable to expect that the bulk of the population, which is not tied to maintaining a nest, will also use large areas. Because the landscape is so heterogeneous, it follows that macaws do use a variety of habitats over the course of a year to satisfy their resource needs.

BROADER IMPACT AND CONSERVATION IMPLICATIONS

It is of little surprise that individual and species variation exists for macaw populations, which has important implications for macaw conservation. Obtaining accurate estimates of densities of population sizes is nearly impossible considering the behavior, mobility and inconsistent detectability of macaws. How does one even define the natural boundaries of a macaw population? Within that population, age and sex cannot be determined, thus even the effective population size cannot be estimated from visual surveys. Counts alone will not provide sufficient information for setting conservation priorities.

This research addresses a critical gap in our knowledge regarding macaw movements; however, even technologies still in development don't have the capability to associate the "where" with the "why". For those breeding individuals that leave their range for brief periods, is there a particular resource that they occasionally need which does not exist within their own range? For those individuals that are not tied to nests, do they have a pattern of movement that repeats itself every few years, or are they temporally random? Our study focused on breeding individuals, but further study is required to understand the spatial and resource needs of the overall population.

At present the landscape is relatively intact and foraging opportunities are plentiful, which is exhibited by the very broad diet, and relatively little time expended actively foraging in a day. There is no indication that food is limited. Although several plants are key foraging species, with such a range of dietary items available, it is difficult to unravel which of those species will be the most important for satisfying nutritional needs in the future. As the landscape becomes more fragmented and suitable habitat decreases, making trips to specific foraging and nesting resources more distant, how will the macaw population be affected?

Superficially, the study area appears to be a contiguous homogenous canopy, however not all regions that were accessible to macaws were used, indicating that habitat which is suitable for macaws is also variable. *Ara ararauna* for example, did not use areas to the west or north of their breeding range. Although there are macaws upriver and in the Manu area which is northwest of Los Amigos, these observations are associated with floodplains and lowland forest. From satellite imagery, the dissected

topography and bamboo-dominated vegetation stretches for hundreds of kilometers, and may in fact be less suitable or even unsuitable habitat for macaws. The distribution and density of macaw populations may be as variable as the landscape, which is important to recognize, especially when doing landscape-level conservation and prioritizing key areas.

Floodplains may have an important role in providing a greater density of nesting sites and diversity of foraging habitat for macaws, but they are a small portion of the landscape, and they alone do not support an entire population of macaws. They are also the first regions to be penetrated and altered by river-bound settlers, and thus unlikely to remain intact. In the context of source-sink dynamics, floodplains and their associated habitats and the large blocks of unfragmented forest that lies beyond may be of equal importance to maintaining the population at a regional level.

Should the existing forest shrink or fragment, leaving only protected areas intact, will these protected areas and habitat fragments be enough to support a viable population of macaws? Protected areas on a map may not be sufficient in size, configuration or even provide the necessary resources. *Ara ararauna* annually migrated to the fragmented landscape during the non-breeding season, rather than migrating to accessible protected areas or even staying within the partially protected and remote breeding area. Even with their unique eyesight, macaws cannot distinguish the boundaries of protected areas, but they can distinguish landscape features, habitats, the resources within them, and can also distinguish between land-use activities and people that pose threats.

It is unlikely that the seasonal visits from an area of low to high levels of human inhabitation and fragmentation indicate a preference for urbanized or altered landscapes. Rather, this demonstrates the strength of the historical importance of these resource patches to macaws (even macaws from other populations) and their tolerance to the level of existing disturbance. This also signals potential conflict over habitat important to both humans and macaws. At present, macaws move relatively undisturbed within this matrix, and even withstand low levels of being shot by Brazil nut farmers. Although harvesting for food, feathers and the pet trade has not been measured in this study area, it does exist, and is a serious problem in more populated regions of the Peruvian Amazon, which is the direction that this region is going as well. How much change to their habitat and pressure from human-related activities can macaws withstand? This threshold has not been established.

Macaws are mobile, intelligent, long-lived, and resourceful birds; all are qualities that bode well for a changing landscape. However, they are also slow to mature, have low fecundity, and their nesting opportunities are limited; all of which have raised concern for their ability to recover if the population declines. Fortunately the macaw populations, however they are to be defined, are relatively healthy in this region of the Amazon due to it being one of the last settled areas of the Amazon. Their current prevailing health masks underlying threats which do exist: their nest trees are cut down for timber and non-timber products or to obtain chicks for the pet trade, they are captured in clay licks for their feathers; some are shot for pleasure, for food, or to scare

them off people's land. These threats are bound to increase as the frontier pushes forward.

The less mobile, actively breeding population would be the most sensitive to a reduction in habitat quality, configuration and size. The greatest immediate threats would be the direct removal of nesting trees, or indirect change in the composition of foraging and nesting habitat. Nesting cavities are limited for all species of macaws. Furthermore, not all cavities are suitable for nesting in terms of security against nest predators and weather. Finally, if nesting individuals must fly further during foraging trips, this forces them to be away from the nest for longer periods of time, and may also affect whether they are even able to obtain sufficient food to support both adults and one or two young.

Breeding pairs with established nests generally nested each year, an activity which is extremely energy-consuming considering that nesting activities and post-nesting parental care essentially consume the entire year. Nest establishment and preparation lasts approximately a month, incubation and nestlings last four months, and the remaining part of the year is consumed by parental care, when the young are completely dependent for food for several months after they fledge, and remain with the parents until they re-nest the following season. The ability to nest each year indicates that the resources needed year-round are sufficient, but will this persist?

Macaws are highly adaptable, but even their ability to alter foraging patterns will not be sufficient to ensure reproductive success. Their requirements for nesting substrates cannot be compromised. If habitat is removed, taking nesting substrates and

foraging trees with it, less individuals will be able to breed successfully. If foraging resources limit breeding to every two or three years, this would significantly impact population growth, and at some point, the population would not be able to maintain itself. Population growth depends on breeding individuals with established nests. Removal of habitat that provides suitable nesting sites, substrates, and foraging resources could irreversibly start a downward trend that is all too real elsewhere in the world.

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APPENDIX A

Relative frequency (F) of plant species consumed by macaws over the year, showing the number of foraging events documented (N) for each plant.

Plant species	*A. ararauna*		*A. chloropterus*		*A. macao*	
	N	**F (%)**	**N**	**F(%)**	**N**	**F(%)**
Bertholletia_excelsa	64	15%	53	30%	11	8%
Hevea_guianensis	50	12%	12	7%	0	0%
Iriartea_deltoidea	42	10%	2	1%	4	3%
Mauritia_flexuosa	32	7%	4	2%	5	4%
Parkia_A39	24	6%	10	6%	2	1%
Euterpe_precatoria	18	4%	2	1%	8	6%
Swartzia_A176	23	5%	2	1%	2	1%
Cecropia_schyadophylla_cf	19	4%	2	1%	1	1%
Sloanea_rufa_cf	15	3%	2	1%	3	2%
Cariniana_decandra	4	1%	6	3%	7	5%
Pseudolmedia_laevis	8	2%	1	1%	6	4%
Eschweilera_A18	7	2%	4	2%	3	2%
Jacaranda_copaia	4	1%	8	5%	2	1%
Inga_A47	8	2%	3	2%	1	1%
Castilla_ulei_cf	7	2%	0	0%	4	3%
Apeiba_membranacea	3	1%	5	3%	2	1%
Couratari_guianensis	0	0%	1	1%	9	6%
Dipterix_micrantha	8	2%	2	1%	0	0%
Pouteria_A73	4	1%	2	1%	4	3%
Phyllocarpus_riedelii	4	1%	0	0%	5	4%
Byttneria_pescapraefolia	0	0%	5	3%	3	2%
Socratea_exorrhiza	8	2%	0	0%	0	0%
Gurania_A25	1	0%	2	1%	4	3%
Inga_A30	5	1%	2	1%	0	0%
Symphonia_globulifera	1	0%	0	0%	6	4%
Terminalia_oblonga	4	1%	3	2%	0	0%
Cedrelinga_cateniformis_cf	3	1%	2	1%	1	1%
Erithrena_poephiana	2	0%	1	1%	3	2%
Matisia_cordata	4	1%	2	1%	0	0%
Parkia_A40	6	1%	0	0%	0	0%
Pouteria_A61	5	1%	1	1%	0	0%
Parkia_C203	5	1%	0	0%	0	0%
Sapium_glandulosum_cf	0	0%	0	0%	5	4%
Caryocar_amigdaleiforme	0	0%	3	2%	1	1%
Couepia_a152	0	0%	0	0%	4	3%
Enterolobium_barnebianum	2	0%	0	0%	2	1%
Hura_crepitans	0	0%	4	2%	0	0%
Manioc_leptotilla	0	0%	2	1%	2	1%
Pseudolmedia_macrophylla	2	0%	1	1%	1	1%

Tachigali_vazquesii_cf	4	1%	0	0%	0	0%
Attalea_butyracea	2	0%	0	0%	1	1%
Cayoponia_A119	0	0%	0	0%	3	2%
Guazuma_trinita	1	0%	1	1%	1	1%
Huberodendron_swietenioides	1	0%	2	1%	0	0%
Inga_edulis_cf	3	1%	0	0%	0	0%
Pourouma_minor_cf	1	0%	2	1%	0	0%
Pseudolmedia_laevigata	0	0%	0	0%	3	2%
Apuleia_leiocarpa	1	0%	1	1%	0	0%
Buchenavia_C201	0	0%	2	1%	0	0%
Cayoponia_A24	1	0%	0	0%	1	1%
Ceiba_pedantra	1	0%	0	0%	1	1%
Ceiba_samauna	1	0%	0	0%	1	1%
Ceiba_x	1	0%	0	0%	1	1%
Cordia_C211	0	0%	1	1%	1	1%
Diospyrus_A97	1	0%	0	0%	1	1%
Ficus_x	1	0%	0	0%	1	1%
Genipa_americana	2	0%	0	0%	0	0%
Inga_coruscans	1	0%	1	1%	0	0%
Meliosma_herbertiir	0	0%	2	1%	0	0%
Ochroma_pyramidale	1	0%	0	0%	1	1%
Oenocarpus_bataua	0	0%	2	1%	0	0%
Otoba_A204	1	0%	0	0%	1	1%
Pouteria_torta	2	0%	0	0%	0	0%
Tynanthus_A178	1	0%	0	0%	1	1%
UN_A159	0	0%	0	0%	2	1%
Acacia_A46	0	0%	1	1%	0	0%
Anomospermun_grandifolium	0	0%	0	0%	1	1%
Anthodiscus_A170	0	0%	1	1%	0	0%
Anthodiscus_peruanus	1	0%	0	0%	0	0%
Bixa_A135	0	0%	1	1%	0	0%
Bochisia_A141	0	0%	1	1%	0	0%
Byrsonima_cf_A91	0	0%	0	0%	1	1%
Byttneria_asterotricha_cf	0	0%	0	0%	1	1%
Byttneria_catalpifolia	0	0%	1	1%	0	0%
Cinchona_C202	0	0%	1	1%	0	0%
Cordia_toqueve	0	0%	0	0%	1	1%
Ducia_A54	1	0%	0	0%	0	0%
Dysidendrum_K5	1	0%	0	0%	0	0%
Enterolobium_schomburgkii	0	0%	1	1%	0	0%
Gallesia_integrifolia	0	0%	0	0%	1	1%
Myroxylon_balsamun	1	0%	0	0%	0	0%
Ocotea_cf_A149	1	0%	0	0%	0	0%
Otoba_A186	1	0%	0	0%	0	0%
Pouteria_A19	0	0%	0	0%	1	1%
Pouteria_A38	0	0%	1	1%	0	0%
Pteryrigota_amasonica	1	0%	0	0%	0	0%

Qualea_C213	1	0%	0	0%	0	0%
Salacia_A168	1	0%	0	0%	0	0%
Schefflera_A160	1	0%	0	0%	0	0%
Tachigali_chrysophylla_cf	1	0%	0	0%	0	0%
Terminalia_amazonica	0	0%	0	0%	1	1%
**UN_A100*	1	0%	0	0%	0	0%
UN_A103	0	0%	0	0%	1	1%
UN_A104	1	0%	0	0%	0	0%
UN_A123	0	0%	0	0%	1	1%
UN_A2001	0	0%	0	0%	1	1%
UN_A34	0	0%	1	1%	0	0%
UN_A56	0	0%	1	1%	0	0%
UN_C204	1	0%	0	0%	0	0%
UN_C209	0	0%	1	1%	0	0%
UN_N1	1	0%	0	0%	0	0%
***UN_x*	29	7%	13	7%	19	13%
TOTAL foraging events	**434**		**174**		**141**	

*UN = Unidentified (but with unique code).

**UN_x= Items unidentified and uncoded, grouped together.

APPENDIX B

Data Collection

Satellite images with 0-5% cloud cover were critical because clouds are not habitat types used by animals. A Landsat 7 ETM+ image (Path 03, Row 069 dated 27 July 2000, SLC on, WGS-84, UTM Zone 19 South) was obtained from the Glovis website. The image had been automatically corrected for radiometric and geometric error, and also terrain corrected (Level 1T). All image analysis was performed with the software ENVI Version 4.5 (ITT Visual Information Solutions).

Image Preprocessing

Bands 1, 2, 3, 4, 5, and 7 of 30 m pixel resolution were stacked together, and the thermal band (Bands 6a, 6b) and the panchromatic band (Band 8) were not used in image analysis. The mountainous regions of the scene (south) were masked out, as this is not macaw habitat. Several image enhancement methods were used to distinguish between feature types. Heterogeneity of the landscape was enhanced by creating a texture band from Band 4 (Variance). An NDVI band and Band-ratio 3/5 were also generated to aid in discriminating between different vegetation types. Band ratios of 4/3, 5/2, 5/4, and 5/7 were also generated for further discrimination of features and to reduce the shadow effect (cite) of topography. To enhance moisture and productivity differences, a Tasselcap band was also generated. New PCA bands were generated using the following pairs of bands: 2 and 5, 4 and 5, 3 and 4, and 5 and 7 (Tuomisto et al. 1994). Other enhancements to aid in interpretation of the image (but not used in the classification) was contrast stretching (Gaussian), convolution filtering (high-pass/low-pass), and pansharpening of Band 4.

Determination of the Land-Cover Classification Scheme

For visual interpretation, several displays were used to guide the identification of features. The best display combination was R: Guassian stretched band, G: band 5 and

B: band 2. The band-ratios displayed as single grey-scale bands were also useful for interpretation. Currently there is no standard classification scheme for landuse/landcover (LULC) for tropical rainforest. Although Anderson's Level I classification scheme can be applied, there would be several differences in Level II classes. By incorporating seasonal changes, McCleary et al. (2008) produced 25 different classes for LULC in the Amazon. Traditionally, habitats were classed as either "inundated" or "not-inundated". Inundated habitats have been successfully detected, and different classes have been defined depending on the study site and knowledge of the area. Swamps have been classed as herbaceous, shrub, palm, or forest swamps. In another study, swamps were classed into backswamp forest, palm swamp, and flooded palm swamp (Kalliola et al. 1991; Hamilton et al. 2007). In the same study, floodplains were classed as forested meander belt vegetation, and successional meander belt vegetation. Rivers, lakes and river bars were later subclassed by McCleary et al. (2008), into low sediment/deep water, medium sediment water, high sediment/shallow water bodies, and wet soil was distinguished from dry soil (as found on river banks). In northern Peru, Salovaara et al., (2005) classify forest habitats into inundated (which include floodplain forest and swamps), non-inundated terrace forests, and non-inundated Pebas forests. McCleary et al. (2008) recognized inundated, mixed, upland non-floodplain, upland ancient floodplain, and upland mixed. However, Lu et al., (2004) further distinguish forests by successional stage, by recognizing mature forest, early successional forest, and late successional forest, as well as agroforesty (monoculture plantations), coffee plantations, and degraded and cultivated pasture. McCleary et al. (2008) have agriculture and non-forest vegetation that would parallel these non-forest classes of Lu et al. The LULC classes used for the classification scheme are a combination of appropriate classes from other studies and field observations (Table B-1).

Table B-1
Possible classes for the Level II equivalent of Anderson's classification scheme.

Level I	Level II (Anderson's)	Level II (Tropical)
Urban/built up land	Residential	Residential
	Commercial and services	Commercial
	Industrial	Mixed urban
	Transportation, communications, and utilities	Paved roads
	Industrial and commercial complexes	Mining
	Mixed urban or built-up land	
	Other urban or built-up land	
Agricultural land	Cropland and pasture	Cropland (rice/corn/potatoes)
	Orchards, groves, vineyards, nurseries, and ornamental horticultural areas	Pasture (degraded/cultivated)
		Coffee plantations
	Confined feeding operations	Chacras (family farms + orchards)
	Other agricultural land	
Forestland (non-inundated)	Deciduous forestland	Early succession (SS1)
	Evergreen forestland	Late succession (SS2)
	Mixed forestland	Mature (M)
		Ancient floodplain (AFL)
		Agroforestry (plantation) (AF)
		Bamboo (BA)
		Open canopy
		Closed canopy
Wetland		Floodplain (pioneer)
		Floodplain (forested)
		Herbaceous swamp
		Palm swamp
		Shrub swamp
		Lake swamp (ingrown)
Water	Streams and canals	High sediment river
	Lakes	Medium sediment river
	Reservoirs	Low sediment river
	Bays and estuaries	Shallow/oxbow lake
Barren land	Dry salt flats	Dry river banks (sand/mud/gravel)
	Beaches	Gravel piles (mining deposits)
	Sandy areas other than beaches	Wet soil
	Bare, exposed rock	Dry soil/dirt road
	Strip mines, quarries, gravel pits	
	Transitional areas	
	Mixed barren land	

Land-Cover Classification

The following data was used in the image classification: the texture band, NDVI band, all four PCA bands (PC band 2+5, PC band 4+5, and PC band 3+4), and all four band ratios (4/3, 5/2, 5/4, and 5/7). These particular band ratios and PC band combinations were found to be useful by a study distinguishing tropical vegetation with approaches similar to the current method. (Trisurat et al. 2000). Two classification methods were used in the analysis of this data. Unsupervised classification (IsoData) was used initially to detect new habitats not detected by visual interpretation. Class minimum and maximum were set at 5 and 20 respectively, and 15 maximum iterations were used.

(Minimum # pixels per class was 1, Maximum Class SD was 1, Minimum Class Distance was 5, and Maximum # Marge Pairs = 2). For the supervised classification, Maximum Likelihood was used because histograms showed that the distribution of DN (digital numbers) was normal. An ROI (Region of Interest) of 17 training sites was created, with a goal of 170 pixels for each ROI class. The following classes did not obtain the recommended number of pixels due to the low frequency of those land covers: shallow water/we soil (61), herbaceous swamp (119), grass (138), urban/non-natural (87), and bare soil (143).

To determine which bands would be the most useful for classification, a training site separability report was calculated for all four PCA bands together, and each PCA band separately to determine which combination would provide better results. The same was done for the band ratios. Separability reports for training sites were highest when all 10 bands were used together, and much higher than when only the original 6 bands (1, 2,3,4,5 and 7) were used. Training sites were edited until pair separation was greater than the recommended value of 1.85. The only pair that had poor separability was the forested meander belt and backswamp forest (1.14). Consulting the initial classified image (Probability Threshold = None, Data Scale Factor = 1.0) resulted in maintaining both classes, even though they had low separability. Open lowland and open upland forest also had a low separability (1.52), and thus were combined in the final classification. The class “slope vegetation” was eliminated from the final classification. To determine the accuracy of the supervised classification method, an Accuracy Report was generated using new ROI’s consisting of >75 pixels for each class (overall accuracy was 61.43%, and the Kappa Coefficient was 0.5867) which was lower than initial classification (accuracy 71.51% (497/695 pixels), Kappa Coefficient was 0.6937), but the separability of the final 15 training sites (ROI’s) was much greater (Table B-2).

Table B-2
Accuracy report showing the User accuracy and Producer's accuracy as well as Commission and Omission of pixels.

Accuracy Report	Commission	Omission	Prod. Acc.	User Acc.	Prod. Acc.	User Acc
Class	(%)	(%)	(%)	(%)	(%)	(%)
palm swamp	3.61	3.61	96.39	96.39	80/83	80/83
shrub swamp	5.88	21.95	78.05	94.12	64/82	64/68
floodplain (pioneer)	43.48	65.33	34.67	56.52	26/75	26/46
palm swamp (flooded)	26.19	19.48	80.52	73.81	62/77	62/84
river bar	15.38	2.53	97.47	84.62	77/79	77/91
water high sediment	43.56	24	76	56.44	57/75	57/101
water low sediment	19.35	10.71	89.29	80.65	75/84	75/93
shallow water	19.48	24.39	75.61	80.52	62/82	62/77
thick herbaceous/shrubby	68.42	68.83	31.17	31.58	24/77	24/76
sparse grass/degraded pasture	15.38	59.26	40.74	84.62	33/81	33/39
mid succession forest	100	100	0	0	0/93	0/66
early succession forest	75.71	79.01	20.99	24.29	17/81	17/70
immature closed canopy (short)	53.13	65.91	34.09	46.88	30/88	30/64
mature closed canopy (tall)	62.7	9.21	90.79	37.3	69/76	69/185
backswamp forest	13.46	21.05	78.95	86.54	90/114	90/104

Post-classification

Several classes were combined after supervised classification was performed. River bank and urban were combined, as was bare wet soil and turbid water, and herbaceous swamp (upland dried lake) and grass, and lowland open canopy and upland open canopy. A majority analysis with a kernel size of 3 x 3 pixels was used to smooth out the "speckled" appearance.

VITA

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